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SYSTEM

OF

DISEASES OF THE EYE.

BY

AMERICAN, BRITISH, DUTCH, FRENCH,
GERMAN, AND SPANISH AUTHORS.

EDITED BY

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VOLUME I.

EMBRYOLOGY, ANATOMY, AND PHYSIOLOGY OF THE EYE.

WITH TWENTY-THREE FULL-PAGE PLATES AND THREE HUNDRED AND SIXTY-TWO TEXT ILLUSTRATIONS.

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PREFACE.

THIS, the first "System of Diseases of the Eye" written in the English language, embraces the most advanced theoretical and practical views on the subject that could be systematically grouped in a single publication.

The editors believe that, by a careful selection of material and by the aid of many and able collaborators, a work has been produced which will take a place in the English language similar to that occupied by the "Handbuch" of Graefe and Saemisch in German and by the "Traité complet" of de Wecker and Landolt in French, and which will be of service not only to ophthalmologists and special students, but also to the medical profession at large.

It is with regret that they make note of the death of their first contributor, Dr. John A. Ryder. To Dr. John Green, of St. Louis, they are under obligation for much kindness and assistance.

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SYSTEM

OF

DISEASES OF THE EYE.

PART I.

EMBRYOLOGY, ANATOMY, AND PHYSIOLOGY OF THE EYE.

DEVELOPMENT OF THE EYE.

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DEVELOPMENT OF THE EYE.

THE mammalian embryo is developed from an egg which at first represents morphologically a single cell. In the course of its development, the substance of the egg divides by means of what is known as indirect or karyokinetic cell-division into two, these two into four, these four into eight cells, and so on, until a globular cell-aggregate is formed. Within this cell-aggregate a cavity, the blastocœle, is soon developed, filled with fluid, surrounded by a cellular wall composed of the cells resulting from the repeated division of the original germ-cell as mentioned above. This spherical cellular wall is essentially an epithelium. The germ is now a hollow globe, known in mammalian embryology as the blastodermic vesicle, the walls of which are constituted by the products of the segmentation of the original egg-cell. At one side of this hollow germ the epithelial wall becomes thicker, owing to the manner in which certain cells of its wall proliferate into its cavity. The thickening or area thus marked out soon becomes oval in outline, and constitutes the germinal area from which the

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embryo is differentiated, together with its enveloping amnion. This epithelial area of the globular germ of mammals, from which the embryo is developed, is sometimes spoken of as the embryonic area of the blastoderm. It very early becomes split up into the three so-called primary germ-layers. Of these the outer, or ectoderm, is the first to appear, after which the entoderm, or innermost, is formed, while the third layer, or mesoderm, appears last of all between the two first-named.

All the structures of the body are developed from the three primary germ-layers of the embryo, viz., ectoderm, mesoderm, and entoderm, of which the first is uppermost and outermost, the second intermediate, and the last lowermost or deepest in position. These three layers are also sometimes spoken of as epiblast, mesoblast, and hypoblast.

From the ectoderm or epiblast, the epidermis, sensory epithelia of the sense-organs, brain, cord, nerves, hair, nails, and superficial dermal glandular structures, the enamel of the teeth, oral epithelium and glands, and epithelium of the nasal chamber, are formed. From the mesoderm or mesoblast, the muscles, bones, cartilages, connective and adipose tissues, heart, blood- and lymph-vessels, blood- and lymph-corpuscles, are formed. The entoderm or hypoblast gives rise to the epithelium of the alimentary canal and of the lungs, to the secretory cells, ducts, and alveoli of the glandular appendages of the alimentary canal, such as the liver, pancreas, etc., while the smooth muscular fibres of the walls of the alimentary canal and the vascular, adenoid, and connective tissues generally, of its appendages, are of mesodermic origin.

All the parts of the eye are developed from but two of the three primary germ-layers. Only the ectoderm or epiblast and the mesoderm or mesoblast take any part in the building up of this important sense-organ; the entoderm or hypoblast is entirely excluded. The lens, retina, optic nerve, pigmented choroidal epithelium; the epithelia of the conjunctiva, cornea, third eyelid; the ocular nerves, the blastema of the nasal duct, the lacrymal ducts and glands, the Meibomian glands, and the eyelashes, arise from the ectoderm. The muscles, vessels, supra-choroid, sclerotic, the deeper layer or corium of the cornea, the anterior layers, vessels, and muscles, the iris, the humors of the eye, and the bones of the orbit, arise from the mesoderm. The adjacent and associated nareal structures arise partly from the ectoderm and partly from the mesoderm.

From a narrow strip of the ectoderm of the embryo, the foundation of the whole of the cerebro-spinal nervous system of the vertebrate body is evolved. This strip of the ectoderm constitutes the medullary plate and lies along and marks the median plane of the future body. Its edges turn upward to form the so-called medullary groove. Along the edges of this groove are also developed, very early, the ectodermal foundations of the sensory ganglia of some of the cranial and of all the spinal nerves. The edges of this groove are gradually lifted upward and grow or bend toward each other; these edges also finally meet and coalesce so as to enclose a

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tubular space, the so-called medullary canal or tube. The tube thus differentiated early separates from the remaining ectoderm, covering the rest of the body along the median dorsal line. It in fact sinks inward or downward along the dorsal line and begins to split off at its dorsal side from the rest of the ectoderm at its anterior end. The ectoderm of either side of the body closes over the medullary tube completely along the dorsal or median line and becomes continuous over the back and forms the foundation of the general epidermis of the head, trunk, and limbs. From the hinder half of the medullary tube in the higher vertebrates the spinal cord is formed, and from its anterior half are developed the brain and sensory epithelium, or essential visual area, and the optic and the cranial nerves. From the fact that the brain and eyes preponderate in importance over everything else at first formed from the anterior end of the medullary canal, the anterior portion of the latter may in the early embryo be called its cerebro-ocular portion. The eye is the only sense-organ the ectodermal foundation of the sensory epithelium of which is at first continuous with the ectodermal epithelium from which the brain is formed.

The eye, within the vertebrate series, has unquestionably arisen primarily as a differentiation of a part of the wall of the primitive cerebro-spinal rudiment or medullary plate of the embryo. Such a differentiation seems from the first to have been anterior, and almost median, to judge from the researches of H. Ayers, Kupffer, and Hatschek upon the development of *Amphioxus*. This conclusion has also lately been fortified by the researches of Kupffer upon the development of the brain in *Amphioxus*, the sturgeon, and the lamprey. In these forms an exceedingly primitive condition of affairs has been preserved. The later studies of Hatschek have tended to confirm the view that the vertebrate eye is a structure that has arisen immediately from part of the lateral cortex of the embryonic brain. Judging from the condition of things in *Amphioxus*, there is scarcely any doubt that the vertebrate eye was functional as such long before it was pushed out from the brain-wall as a lateral diverticulum, and before even the development of an optic stalk. This view seems to be supported by the fact that the pigmentary screen representing the first trace of the pigmented choroidal epithelium in the vertebrate series lines the inner face of the anterior portion of the nervous system of *Amphioxus* at the points where an ocular function is first developed. The tissues which envelop the brain and nervous axis in *Amphioxus* and the brain itself are in life quite transparent, so that there was no necessity for the evolution of the series of transparent humors, of a refracting apparatus, or of a camera in the form of an eyeball with its automatic shutter or iris, and muscular apparatus of accommodation, and adjustment for direction, as seen in higher types. In this lowly and primitive type of ocular apparatus of *Amphioxus*, without an eyeball, a sharply-circumscribed retinal area, an optic nerve, ocular muscles and nerves, lens, or any of the usual accessories of the vertebrate eye, we very probably have the promise and possibility

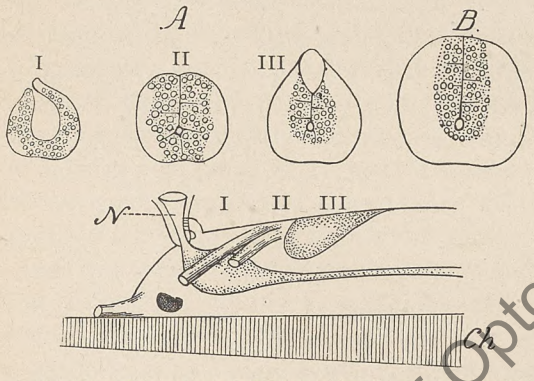
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of the evolution of the later far more complex visual mechanism of higher vertebrates.

Ayers has ingeniously suggested that the median or parietal eye, so fully described by Spencer, and occurring in reptiles, batrachians, and fishes, as a more or less well developed organ or vestige of one, was also derived ancestrally from the extension forward and upward into a median dorsal position of the primitive lateral ocular areas of the brain-wall of *Amphioxus* or of some similar ancestral form. The primitively undivided median position of the olfactory area of certain low forms, as the sturgeon, where it also at first forms part of the brain-wall, as shown by Kupffer, also lends support to the belief that the paired eyes of the higher vertebrates were primarily nearly median in their origin.

If these views are correct, they have the advantage of bringing the ontogenetic or embryonic history of the eye into perfect parallelism with its phylogenetic history, or the series of transformations it has suffered in the course of the evolution of vertebrates. In Fig. 1, the very primitive relations of the oval ocular patch at the lower anterior part of the brain of a very young *Amphioxus* are shown, as well as the relations of this ocular patch in the infero-lateral brain-wall to the cavities of this very primitive condition of the vertebrate brain. The dilatation below I, lower figure, is clearly the homologue of the third ventricle of the brains of other vertebrates, in which the space within the brain under III is as clearly homologous with the fourth ventricle, with its thin roof, as seen in other vertebrata. It will be seen that we have in this arrangement an optic organ which has not yet developed to the point of being pushed out from the sides of the brain, though Dr. Ayers has informed me that there is a slight thinning and outpushing of the lateral walls of the brain of the young of this creature at this point. The parts are in such relations to each other that it is clearly possible to imagine them as representing a stage of eye-development still more primitive than any that is at the present time permanent or even manifested temporarily by any other vertebrate.

FIG. 1.



Side view (lower figure) of anterior end of central nervous system of a young *Amphioxus*, three millimetres long, representing the brain, cranial nerves, and notochord, *Ch*, with a dark reniform spot at the side below, indicating the position of the ocular area. Cross-sections of the brain, I, II, III, *A*, at corresponding points, I, II, III, in lower figure. *B*, Cross-section of spinal cord. (After Hatschek.)

Between this very primitive state of the vertebrate eye and that of the fully-developed one of the higher vertebrates, a great many additional

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features have been intercalated, and it will be our purpose to trace the development and describe the method of accretion of these new features in the course of the following pages.

In the very earliest form of the vertebrate eye, therefore, the conclusion seems to be established that the ectoderm alone was involved. This is still further established by the recent discovery by Eycleshymer (*Journal of Morphology*, 1893) that the eyes of the embryo of *Necturus* before the closure of the medullary groove are already defined as a pair of pigmented and thickened areas of the ectoderm at the anterior end of the medullary plate. The pigment here, however, is developed within the cells of the ectoderm itself, and is not at first a separate layer, as it becomes at a later stage in the development of the same animal. It is also to be borne in mind that the diffused pigment-granules seen in these paired ocular patches at the anterior end of the medullary plate of *Necturus* lie within the substance of the ectoderm cells of those patches. This general diffusion of pigment-granules through the cells of the body of the embryo is characteristic of batrachians, but is exceptional among other vertebrate forms.

In the embryo of the rabbit of the ninth day the anterior end of the medullary groove begins to widen at the point where the eye will be developed before the groove itself is here closed and separated from the ectoderm covering the head. In fact, in an embryo of the rabbit of the age mentioned, the first traces of the eyes have already appeared as obvious lateral expansions of the anterior end of the medullary plate and before the latter has closed dorsally on the median line. The development of the eyes of mammalia is therefore seen to be very precocious,—more so, in fact, than in birds, as will appear later.

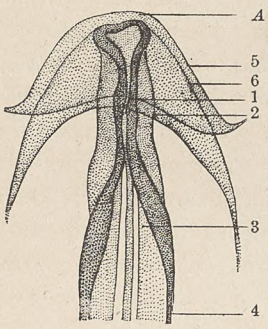
The earliest trace of the optic region of the brain or first embryonic cerebral vesicle of vertebrates above *Amphioxus* is the broadening of the anterior end of the medullary plate or tract of ectoderm from which the brain and the cord are formed. As soon as the medullary groove closes, a process which always takes place first of all at the anterior end of the medullary plate, by an upfolding of its opposite halves and a bending of those halves toward one another till their edges meet and fuse along the median dorsal line, there is at once developed a tendency for the anterior end of the cerebro-spinal rudiment to enlarge. This enlargement is mostly at first in the direction of the transverse and vertical diameters of the anterior end of the medullary canal or tube, as the common, but now involuted, ectodermal rudiment of the brain and eyes may be called. The detailed history of this region of the medullary canal differs very greatly in the different vertebrates. For example, there is at first a complete obliteration of the medullary canal in this region in the embryos of bony fishes, lampreys and *Lepidosteus;* in consequence of which, after the closure and detachment of the medullary plate from the rest of the ectoderm of the dorsal region, this important organ may be called a medullary cord more properly than a canal. In these lower types of vertebrates—fishes and batrachia—

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the cerebro-ocular portion of the cerebro-spinal rudiment is also proportionally much shorter than in the three higher series of vertebrates,—namely, reptiles, birds, and mammals,—in which this region extends for almost half the length of the embryo by the time the latter has been first definitely outlined. In that we are more especially concerned with a consideration of the development of the eyes of the higher series, especially the mammalian, to which man belongs, we may at once turn to a more detailed description of the steps by means of which the anterior or cerebro-ocular portion of the medullary canal is transformed in that series into the essential foundation of the organ of vision. Inasmuch as the embryology of the bird illustrates this part of the subject very well, we begin with it.

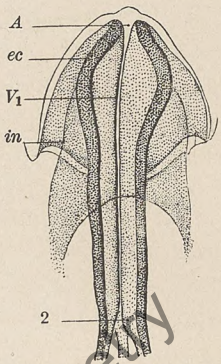
In Fig. 2, representing the anterior end of an embryo chick of about the

FIG. 2.



Head of embryo chick of 23 hours, viewed from above.—*A*, anterior end of head; 1, superior margin of medullary fold of right side nearly in contact with its fellow of the opposite side; 2, lateral limit of wall of medullary or neural tube; 3, point posteriorly where the edges of medullary groove have not yet united; 4, widely-open posterior portion of same; 5, lateral ectoderm of head; 6, lateral limit of foregut. Enlarged 30 times. (After Duval.)

FIG. 3.



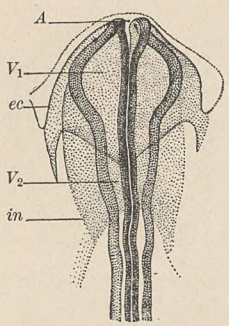
Head of embryo chick of 25 hours, viewed from above.—*A*, anterior open extremity of cerebro-spinal canal; *ec*, lateral limit of the outer face of the neural canal; V_1, first cerebral vesicle; *in*, lateral limit of foregut; 2, point where the edges of the medullary groove have not yet fused in the middle line. Enlarged 24 times. (After Duval.)

end of the first day, the edges of the medullary groove are just about closing and coalescing at a point a very little way behind the extreme anterior end of the embryo itself. The forward end of the medullary canal is still open, and the edges of the medullary plate do not finally close at this point until about six hours later. In fact, at this stage the cerebro-ocular portion of the medullary canal is still open anteriorly and posteriorly. It is not until about two hours more have elapsed that the development of the anterior part of the cerebro-ocular portion of the medullary plate has progressed so far as nearly to close off this portion of it from the exterior, as shown in Fig. 3. This stage, however, is interesting from the fact that we now have for the first time in the bird distinct traces of the eyes. At the point *ec* the medullary canal is seen to be distinctly dilated in excess of the

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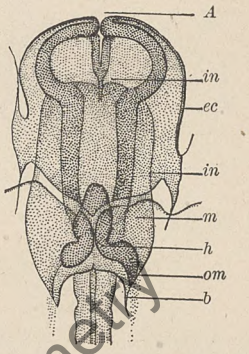
regions behind it. This dilatation is the first indication of the differentiation of the ocular portion of the ectodermal cerebro-spinal rudiment. In another representation of the anterior end of an embryo chick another hour older than the last (Fig. 4) this anterior dilatation, V_1, is still more marked, and indications of a second less marked dilatation of the medullary canal, V_2, may also be noted, with even a trace of a third dilatation behind the latter. These three primary dilatations of the medullary canal constitute the three primary or embryonic cerebral vesicles. Of these, the first is intimately associated with the future development of the retina, the eyeball, and the third ventricle of the brain; the second, with the development of the cerebral peduncles, optic thalami, optic tract, geniculate bodies, and aqueduct; while the fate of the third is to become the fourth ventricle, cerebellum, pons, and medulla oblongata. In Figs. 5 and 6, representing

FIG. 4.



Head of embryo chick of 26 hours, from above.—*A*, anterior end of head, neural tube not yet quite closed anteriorly; V_1, first cerebral vesicle; *ec*, outer lateral surface of ectoderm of head; V_2, second cerebral vesicle; *in*, lateral limit of foregut. Enlarged 26 times. (After Duval.)

FIG. 5.



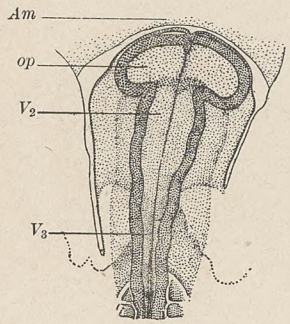
Head of chick embryo of 27 hours, viewed from above.—*A*, anterior end of head; *in*, anterior and lateral limit of foregut; *m*, mesoderm of pericardiac cavity; *h*, paired rudiment of heart; *om*, omphalomeseraic veins; *b*, margin of opening into foregut. Enlarged 28 times. (After Duval.)

still more advanced stages of the anterior ends of chick embryos, the fusion of the opposite edges of the medullary plate has been about completed; but it is obvious that the first cerebral vesicle, *op* (Fig. 6), is expanding at a relatively much more rapid rate than the parts of the medullary canal or cerebro-spinal rudiment behind it. In fact, there is now in progress a very rapid lateral dilatation of the anterior end of the medullary canal, and it may be said that the foundations of the *primary optic vesicles* have now been established as a pair of diverticula from the sides of the anterior end of the hollow cerebro-spinal rudiment. In Fig. 7, representing the anterior end of an embryo of the rabbit of a stage about parallel with that of the chick embryos just described, the same relation of parts is seen; the primary optic vesicles, *op*, are conspicuous, and the three primary cerebral vesicles are also distinctly evident, though the medullary groove is not yet closed. There is here the same kind of epithelium forming the walls of the primary

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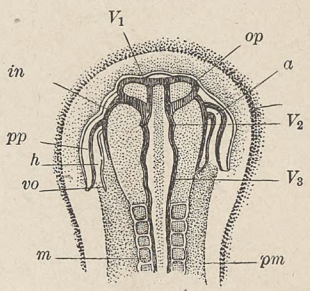
optic vesicles and of the primary cerebral vesicles as in the embryo chick. From the cells of the walls of the optic vesicles the ganglion-cells of the retina, the rods and cones, and the axis-cylinders of nerve-fibres of the first portion of the optic nerve are to be differentiated as the result of a complex series of histological transformations. From parts of the walls of the optic vesicles the pigmented epithelium of the choroid, part of the iris, and the embryonic optic stalk are also to be formed. The steps, however, by which these changes are brought about proceed in a manner analogous to those that we have already traced in the progress of the differentiation of the medullary canal itself,—namely, by the dilatation of one part and the constriction of another, or the fusion of two adjacent parts of the epithelial rudiments concerned at another point. Where such dilatation occurs locally and a vesicle is pushed or extended outward, the process is spoken of as

FIG. 6.



Head of embryo chick of 29 hours, viewed from above.—*Am*, head-fold of amnion; *op*, optic vesicle; V_2, second cerebral vesicle; V_3, third cerebral vesicle. Enlarged 22 times. (After Duval.)

FIG. 7.



Anterior end of rabbit embryo of 8 days and 14 hours, viewed from above and enlarged 15 times.—*op*, optic vesicles; V_1, V_2, V_3, first, second, third embryonic cerebral vesicles; *in*, outer limit of foregut; *pp*, anterior part of body cavity, lateral pericardiac spaces; *h*, left half of heart; *vo*, left omphalomeseraic vein; *a*, anterior or aortic end of right half of embryonic heart; *m*, somites, myotomes, or "protovertebræ;" *pm*, parietal mesoblast of sides of body. (Reduced from Kölliker.)

evagination; where such a process pushes and extends a membrane inward into the form of a cup or sac, it may be spoken of as invagination. Where fusion of two parts takes place along their edges and along a line, as, for example, along the coalescing edges of the upturned borders of the medullary plate, such a process may be spoken of as concrescence. These processes, variously modified and supplemented by cell-differentiation and cell-proliferation, constitute the principal methods by which the complex transformations of the mammalian embryo and of its parts are effected.

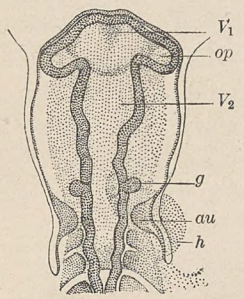
These statements are especially well illustrated by the events of the subsequent history of the development of the eye. In Fig. 8, for example, the optic vesicles, *op*, are beginning to show evidences of constriction at their bases so as to form a hollow stalk, a condition which becomes still more obvious in Fig. 9. In fact, the optic vesicles now appear smaller than the intervening median portion, V_1, representing the growing first cere-

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bral embryonic vesicle. This constriction of the basal part of the optic vesicle leads to the differentiation of the hollow optic stalk as distinguished from the more dilated, distal, optic vesicle proper. This differentiation of the distal and basal parts of the optic vesicles is the first indication of a growing distinction between what is to become the foundation of the eyeball and of what is to direct the course of the development of the ingrowing portion of the optic nerve, since the optic stalk is not directly transformed into the optic nerve, as we shall learn later. The tendency for the optic vesicles to be pushed slightly backward distally is also obvious now, as well as their close apposition against the inner face of the superficial ectoderm of the head, as shown in Figs. 6, 8, and 9.

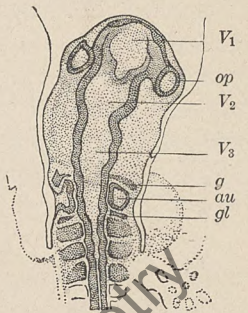
While the last two figures represent the three primary cerebral vesicles very strongly accentuated as V_1, V_2, V_3, it is obvious that there are evidences

FIG. 8.



Head of embryo chick of 32 hours, viewed from above.—V_1, first cerebral vesicle; *op*, optic vesicle; V_2, second cerebral vesicle; *g*, facial and auditory ganglion; *au*, auditory ganglion; *h*, heart. Enlarged 22 times. (After Duval.)

FIG. 9.



Head of embryo chick of 38 hours, viewed from above.—V_1, first cerebral vesicle = third ventricle; *op*, optic vesicle; V_2, second cerebral vesicle; V_3, third cerebral vesicle = fourth ventricle; *g*, facial ganglion; *au*, auditory vesicle; *gl*, glosso-pharyngeal ganglion. Enlarged about 20 times. (After Duval.)

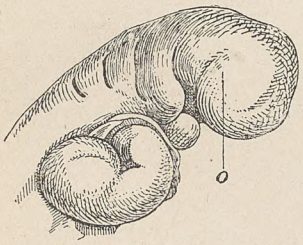
of a subdivision of V_3 into a series of segments by at least five very slight subordinate constrictions. These subordinate subdivisions of the posterior portion of that part of the medullary tube which is to form the brain are indicative of the segmental nature of the posterior portion of that organ. And, since it is possible to trace a tendency toward segmental differentiation of the cerebro-spinal embryonic axis into the trunk, it does not seem improbable that the indications of segmental differentiation in the posterior part of the rudiments of the brain are, like those of the trunk, traceable to the originally segmental nature of this part of the head. This is rendered quite certain by the fact that recent research upon the development of the head of the shark-like fishes shows a segmented condition in the early stages directly comparable to that which is so very obvious in the trunks of vertebrate embryos as blocks or segments of mesoderm, as shown in Fig. 7 at *m*. The segmented or metameric nature of the head of all vertebrate embryos is now a well-recognized canon of morphology, but the facts upon

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which this conclusion is based have been almost entirely disclosed by embryological research, this doctrine no longer deriving any essential support from the consideration of the segmentation of the hard or bony part of the adult cranium. It is a singular fact, however, that in the higher vertebrates, birds and mammals, in which the early steps of development have been much condensed or abbreviated, there seems to be no very clear record left of the exact number of cranial segments when the embryonic history of the soft parts is examined. In the shark-like fishes there seems to have been but little abbreviation or elision of primitive embryonic features, and it is to them that embryologists have been compelled to appeal in order to get a clear notion of the history of the cranial nerves, and especially of the relations of some parts of these primitive cranial segments to the development of the muscles that move the eyeballs, as we shall learn later.

The three primary embryonic vesicles are not to be confounded with the single segmental or metameric elements of the nervous system, of which the third cerebral vesicle is so obviously built up. It is far more probable, indeed, that the two anterior cerebral vesicles will ultimately prove to be embryologically composite structures, and be found to be built up of metameres or segments, the boundaries between which have become obscured by the manifold ways in which their development has been abbreviated and modified in higher types.

FIG. 10.



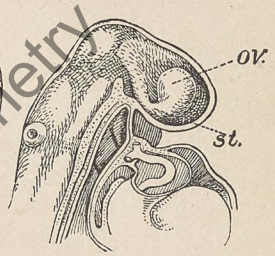
Oblique view of the head and forepart of trunk of a human embryo of 12 to 15 days. The almost globose forepart of the head is prominent laterally at *o*, where the optic vesicle of the right side rests against the cephalic ectoderm. The form of the mouth is also obvious, with the mandibles not yet completely joined in the middle line. Enlarged 20 times. (After His.)

FIG. 11.



Side view of the head of a human embryo of about the same age as the preceding. Enlarged 20 times. (After His.)

FIG. 12.



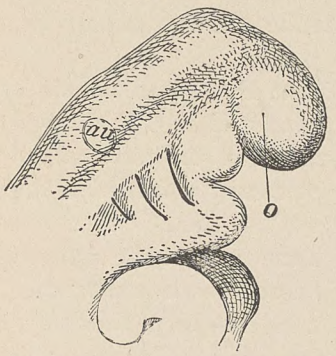
Side view of the head of a human embryo of the same age as the two preceding, but with the outer ectoderm and mesoderm of the head removed to show the form and volume of the brain and cord and the very early form of the optic vesicle or rudiment of the eye, *ov*, and its stalk, *st*. Enlarged 20 times. (After His.)

The embryonic transformation of the cerebro-ocular region of the medullary plate in the human embryo is very similar to that traced and illustrated above in the case of the embryonic bird. The accompanying Figs. 10 to 14 show the heads of human embryos ranging in age from twelve to twenty days. In the surface views, Figs. 10, 11, and 13, there are still

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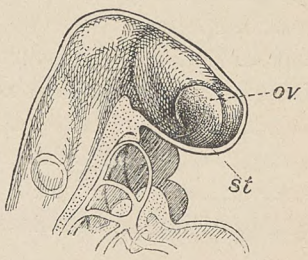
no outward indications of visual organs except a slight prominence at *o*, which indicates the position externally of the underlying optic vesicles, now quite developed to, or slightly beyond, the condition shown by the oldest bird embryo thus far described. Upon the removal of the external ectoderm of the head, as has been done in Figs. 12 and 14, which correspond respectively to Figs. 11 and 13, the optic vesicles, *ov*, are disclosed,

FIG. 13.



Head of human embryo of 18 to 20 days, viewed from the side. Enlarged 20 times, showing the three anterior visceral clefts and the lateral thickening at *o*, indicating the position of the primitive optic vesicles or rudiments of eyes. (After His.)

FIG. 14.



Side view of the head of a human embryo of about the same age as the foregoing, with the ectoderm and mesoderm of the head removed to display the form and great relative volume of the brain and cord, as well as the optic vesicle, *ov*, with its stalk, *st*. The primitive aortic arches are shown in the lower part of the figure. (After His.)

showing their attachment, also, to the sides of the anterior lower border of the first cerebral vesicle by means of a thick stalk, *st*. These stages of the development of man correspond pretty closely with the second day of the chick, and, as viewed from the side, they show very clearly the abrupt flexure or bend downward of the anterior end of the cerebro-spinal rudiment, which has carried all the other surrounding organs along with it. This bend is known as the *cranial flexure*, and has an important bearing on the development of the face. This cranial flexure is common to all the vertebrates above *Amphioxus*,[1] but is most marked in the higher series. It is noteworthy that the eye in the human embryo at this stage is entirely lateral in position. It is only in consequence of the great lengthening of the optic nerve and stalk, and the correlated shifting and development of the adjacent organs, that the eye is finally brought round into an anterior position. The eye at this stage in man is, in fact, in the position in respect to the axis of the body that is permanent in the great series of lower vertebrates, or the fishes and batrachians. This fish-like character of the early human embryo is also very clearly shown by the obvious visceral or gill clefts visible on the sides of the future upper-neck-region in Figs. 10, 11, and 13. The traces of the first pair

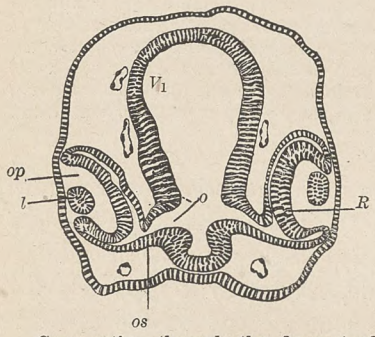
[1] Even *Amphioxus* shows traces of the development of the cranial flexure in the embryo, according to Kupffer, but the flexure disappears before the attainment of full growth.

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of sense-organs, or olfactories, in these figures are still less obvious externally than the development of the foundations of the eyes, as disclosed by the reconstructed Figs. 12 and 14. The face, as a whole, is still without any hint of resemblance to that of the adult. The mouth is almost quadrangular in outline, and the oral and nasal epithelial tracts are continuous, and in no way differentiated from one another, judging from external appearances alone. The foundations of the brain and of the eyes lie in almost immediate contact with the general ectoderm covering the head, and, taken together, now constitute the principal part of the substance of the latter.

A cross-section carried through the point *o*, Fig. 13, would disclose a relation of parts somewhat similar to that shown in Fig. 15 through the first cerebral vesicles and eyes of a chick embryo of the early part of the third day, though the latter figure really represents a condition slightly more advanced. In Fig. 15 the ectoderm of the head is seen to lie in close contact with the eyes laterally and with the walls of the first cerebral vesicle, V_1, dorsally and ventrally. The optic stalk *st* has been decidedly narrowed, though still hollow, as indicated at *o*. The optic vesicles are in fact now pedunculate. A change has also taken place in the relations and form of the epithelium of the distal extremity of the optic vesicle. This distal extremity is no longer convex exteriorly, as shown in Figs. 8 and 9, but concave. The distal extremity of the primary optic vesicle has in fact been invaginated so as partially to obliterate the cavity within, as is well shown in Fig. 9 at an earlier stage. The result of this second change in the optic vesicle is to produce a concavity or vesicle on the outer face of its distal extremity so as to form the so-called optic cup, or secondary optic vesicle, in contradistinction to the primary one. This secondary optic vesicle or optic cup now becomes the foundation of the eyeball, or globe.

Fig. 15.



Cross-section through the forepart of the head of an embryo chick of 52 hours, showing the completion of the involution of the secondary optic cup. (Reduced, after Duval.)—*os*, optic stalk; *o*, canal in same connecting the now nearly obliterated cavity of the primary optic vesicle with the first cerebral vesicle, V_1; *op*, optic cup; *l*, lens; *R*, retina. None of the mesoderm is shown except the walls of the blood-vessels. Enlarged 30 times.

The changes which are a prelude to the condition shown in Fig. 15 are well illustrated by Fig. 16, which represents the relations of the ectodermal layers which enter into the formation of the eye of a chick embryo somewhat younger than that shown in the preceding figure. The ectoderm, *h*, is shown as lying close against the outer extremity of the optic vesicle, and where it comes in contact with the latter is slightly thickened as the rudiment of the lens *l*, which lies in close contact with the wall, *r*, of the outer end of the optic vesicle. This part, *r*, of the wall of the primary optic

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vesicle is destined to become the retina, whilst the distal part of *p*, or the wall of the optic stalk nearest the retinal rudiment, is destined to become the pigmented epithelium next the supra-choroid. The proximal part of the wall of the stalk, *p*, becomes the definitive hollow optic stalk, with a passage leading from the cavity of the primitive optic vesicle to the cavity within the brain-wall, *vh*. This continuity of the cavity of the first cerebral vesicle and the primary optic vesicle will be self-evident from an inspection of Figs. 8 and 9. As, however, the retinal wall of the optic cup is pushed inward, as in Fig. 15, the cavity of the primary optic vesicle is obliterated, since this secondary retinal vesicle or optic cup, as we may call it, is expanding inward, outward, upward, forward, backward, and downward, so as to develop a spherical enlargement of itself as the foundation of the eyeball and its included vitreous cavity within the cup. While this process is in progress, the retinal wall of the optic cup is thickening. The retinal wall is also seen to be continuous with the outer wall of the optic cup at its rim, as shown in Fig. 15. The result of this is that the walls of the secondary optic vesicle or cup are double; this doubling is the result partly of a thrusting of the wall of the outer extremity of the primary optic vesicle into the hollow proximal or stalk portion of the vesicle, accompanied by an expansion of the stalk portion, next the retinal vesicle, over the latter. The outer wall of the double-walled cup thus formed becomes the pigmented or choroidal epithelium. The relations of the double walls of the optic cup at this time have been not inaptly compared to the relations between the double walls of a Tantalus's cup with the space between them.

FIG. 16.

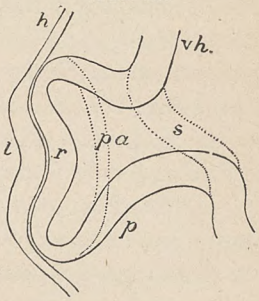


Diagram showing relations of the ectodermal rudiments of the eye in an embryo chick at the end of the second day. Enlarged 75 times. (Reduced from Kölliker.)—*h*, superficial ectoderm; *l*, portion of the latter which will become the lens; *r*, retinal, *pa*, choroid epithelium; *p*, optic stalk; *s*, brain-wall; *vh*, anterior cerebral vesicle.

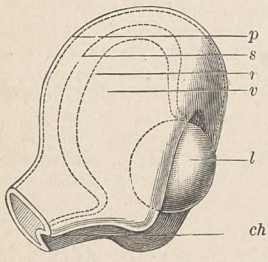
The lens-rudiment is meanwhile being invaginated from the ectodermal area, *l*, Fig. 16. In Fig. 15 this involution has been completed, and the lens now lies free in the cavity of the retinal cup, the latter already retreating from contact with the lens, thus giving rise, in the bird, to a space between the lens and the retina, that represents the vitreous body. The vitreous cavity is already very obvious in Fig. 15, whereas in the younger stage represented by Fig. 16 the rudiment of the lens *l*, and the retina *r*, are still in contact. In Fig. 15 the origin of the optic stalk from the ventral portion of the wall of the first cerebral vesicle is also very obvious. Upon the first appearance of the primary optic vesicles the origin of the optic stalks from the brain-wall is not so obviously ventral, but almost lateral; in fact, there is very strong ground for the belief that the ventral position of the origin of the optic stalk in the vertebrates is a secondary and not a primary characteristic. The optic nerve, if it is to be homologized serially with the other cranial and spinal nerves, must,

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on account of its function, be regarded as sensory. This view of its nature is strongly supported by the early history of its ganglionic rudiment or retina, which, before the closure of the medullary plate, is now known to lie quite near the lateral margin of the latter, or in the analogous position of the serially homologous rudiments of the ganglia of the sensory roots of the spinal nerves along the course of the spinal cord. Since these arise from differentiations developed along the extreme outer edges of the medullary plate, the neural crest of Balfour is probably made up of the rudiments of these ganglia that have fused along the line of closure of the medullary canal, as contended by Beard. If the retinal area at the anterior end of the medullary plate is serially homologous with the rudiments of the sensory ganglia of the spinal nerves, as would seem to be indicated by its lateral position in some forms (*Necturus*), Miss Platt's contention that the optic nerve is primarily of dorsal origin gains in probability, and her ingenious explanation of the change in the ultimate position of its origin also becomes more plausible. Finally, it may be added that the primarily centripetal ingrowth of the axis-cylinder fibres of the ganglionic cells of the retina, as established by recent investigators, is further proof of the same conclusion.

If the whole secondary optic cup and stalk could be removed and isolated from an embryo chick somewhat older than that shown in Fig. 15, we should get a structure which in perspective when viewed from in front obliquely would appear very much as in Fig. 17. In this condition, however, the edges of the cup would begin to bend inward toward the lens all round except below at *ch*, the position of the so-called choroid fissure. At this stage the retina, *r*, is already markedly thicker than the pigmented layer, *p*. The space, *s*, between the retina and the pigmented layer is becoming reduced. The vitreous cavity, *v*, is spacious. The choroid fissure leads from below into the vitreous space. This choroid fissure is also extended as a groove on the under side of the optic stalk, *op*, for some distance inward from the lower margin of the optic cup. This figure must be supposed to be drawn from an eye in the stage of the secondary optic cup with all the investing mesoderm cleared away, and with the future corneal area of the ectoderm on its outer face lifted off, together with the neighboring ectoderm of the head. It represents in a generalized form the relations of all the structures of ectodermal origin that enter into the formation of the vertebrate eye and that lie within the sclerotic and the cornea, both of which latter are developed considerably later.

FIG. 17.



Enlarged model or reconstruction of secondary optic cup of a vertebrate embryo. (Modified from Hertwig.)—*p*, outer wall of cup destined to become the pigmented choroidal epithelium; *r*, its inner wall, or retina; *s*, temporary space between the two walls; *v*, vitreous space; *l*, lens; *ch*, choroid fissure; *op*, hollow stalk of secondary optic vesicle, with groove on the under side continuous with the choroid fissure, *ch*, on the under, outer border of the optic cup.

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The histological changes which accompany the differentiation of the parts of the eye, as these are laid down, are very remarkable. For example, it may be said that the whole of the cerebro-ocular portion of the medullary plate in the very earliest stages of its differentiation is essentially a continuous, simple epithelium made up of columnar or cubical cells. In the course of the foldings and transformations which have attended the evolution of the eye and brain up to the point illustrated by the last few of our figures, histological differentiation has been going on at a very rapid rate. These changes are more profound and important than one is at first disposed to think, as the following statement of fact will disclose.

The retinal area begins to thicken as soon as the secondary optic vesicle or cup begins to be involuted. This thickening of the retina is the result mainly of the rapid multiplication of the cells on what is now its convex and future outer face. While the constituent cells of the embryonic retina still show a tendency to remain columnar, they soon become piled upon one another in layers in consequence of this multiplication, so that all the cells do not extend entirely through its thickness. The retina thus comes at a very early period of its development to be composed of a number of superposed layers. These layers very soon become broken up into groups, of which at least three are developed quite early. Of these the innermost, or that upon its concave side, is destined to become the ganglionic layer of the retina, the next is the middle cellular layer, and the outermost is the true sensory epithelial layer, from some of the cells of which are developed those peculiar sensory extensions known as the rods and cones. The intervals of separation between these layers soon become filled up with finely reticular or granular layers of substance, forming the foundation of the so-called "inner and outer molecular layers" of the adult retina. The first of these molecular layers to appear in the embryo seems to be the "inner" one. From what is now known of the history of the inner or retinal wall of the optic cup, there can scarcely be any doubt that it really represents a portion of the primitive brain wall or cortex precociously projected outward upon the optic stalk, where its histological elements undergo a most complex series of formal differentiations that are analogous to some of those that go on within the developing brain. If it is admitted that the retina is a precociously separated portion of the brain wall or cortex, we are in some measure enabled to understand the peculiar mode of development of the optic nerve, and also why it is doubtful whether this pair is a true cranial one. This difficulty in great measure disappears, however, if it is supposed that the primary retinal area is primarily lateral or at the edge of the medullary plate, and therefore ganglionic in position when its first traces appear in the embryo.

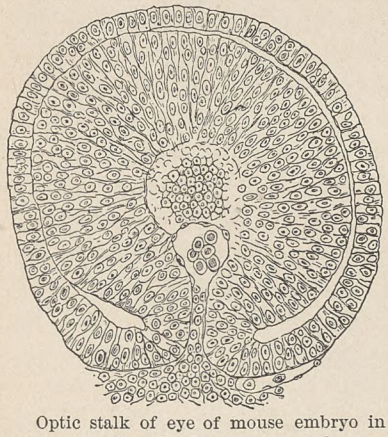
The changes which go on in the shapes and relations of the cells forming the outer wall of the secondary optic vesicle are much simpler. Here there is no proliferation of cells tending to thicken this wall; on the contrary,

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there is a steady diminution of thickness of the outer wall, which eventually becomes reduced to the condition of a simple pavement epithelium composed of a single layer of cells. These cells are so arranged in relation to one another that each undergoes extension at an equal rate in every direction in the area of the membrane of which it is a part, so that the equal pressures it exerts in every direction are met by equal resistances from its fellow-cells that surround it. Since six cells is the usual number that surrounds a single cell, the pressures and interactions due to growth develop a tendency in each of these cells to assume a six-sided or hexagonal form. Before their extreme flattening, however, has been attained, these cells of the outer wall of the optic cup begin to develop granules of pigment within their substance. In this manner the cells of the outer wall become transformed into the pigmented layer or choroidal epithelium of the eye. The very great differences already presented during the early stages of the development of the inner and outer walls of the optic cup are well shown in Figs. 38 and 39 at *r* and *p*.

In Fig. 18 we have represented a cross-section of the optic stalk of an embryo mouse, showing the generally columnar character of the cells of the very thick inner layer continuous with the retinal or inner layer of the secondary optic cup. The outer layer, especially on the upper side of the figure, is seen to be composed of columnar or cubical cells in a single layer, and this is continuous with the outer wall or pigmented layer of the optic cup. On the under side of the optic stalk there is a deep fissure caused by the inflection or infolding of the ventral portion of the originally tubular optic stalk, into which mesoderm has been intruded along with a blood-vessel, and in which a group of blood-corpuscles are lying free. The endothelium of this vessel is also well marked as a single layer. This fissure is the extension inward upon the under side of the hollow optic stalk of the choroid fissure of the optic cup. Into it have been intruded a vessel, the *arteria retinæ centralis*, already noted, and a strip of mesodermal tissue continuous with that which immediately invests the stalk externally. The great differences in the thicknesses of the inner and outer layers of the optic stalk are here as noteworthy as the differences between the thicknesses of the inner and outer walls of the optic cup itself. It is also worthy of note that the originally tubular canal of the optic stalk, as shown in Figs. 8 and 9, has now been almost com-

FIG. 18.



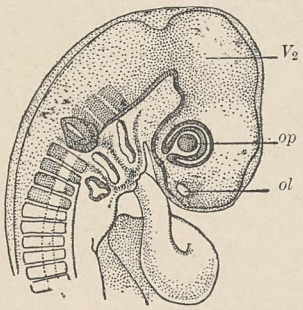
Optic stalk of eye of mouse embryo in cross-section, showing lumen of central artery intruded into the continuation of the choroid fissure ventrally; thick inner wall continuous with retina; thin outer wall continuous with pigmented choroidal epithelium of the secondary optic cup. Enlarged 200 times. (After Kessler.)

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pletely obliterated by the inflection of its inferior wall within the superior outer wall, so that the two are in contact almost the whole way round. The continuity of the inner and outer layers of the stalk along the edges of the extension of the choroid fissure upon the optic stalk is also very evident. The edges of this groove ultimately close, so that little or no trace of it is left, a condition of affairs that is still further modified upon the ingrowth of the first-developed fibres of the optic nerve toward the brain, as we shall learn later.

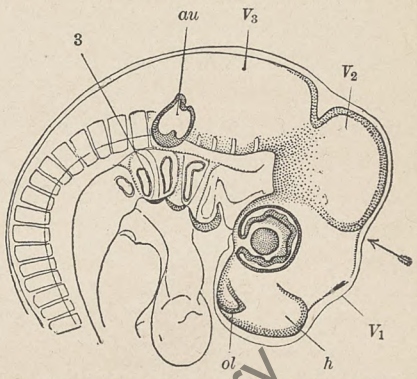
A very vivid conception of the position and relation of the choroid fissure can be got from an inspection of Figs. 19 and 20, representing the heads of chick embryos of the third day of incubation as viewed from the side.

FIG. 19.



Side view of head of an embryo chick of 52 hours. Enlarged 14 times. (Reduced from Duval.)—*op*, optic cup from exterior, showing choroid fissure; *ol*, olfactory pit; V_2, second cerebral vesicle; heart, auditory vesicle, and three visceral clefts are also conspicuous.

FIG. 20.



Side view of head of an embryo chick of 68 hours. Enlarged 14 times, to show the relations of the eye to the other cerebral structures and the open choroid fissure. (Reduced from Duval.)—*au*, ear; 3, third visceral cleft, 1 and 2 in front of, and 4 behind it; *h*, cerebral hemisphere; V_1, V_2, and V_3, first, second, and third cerebral vesicles; *ol*, olfactory pit. The somites of the neck, head under V_3, and trunk are also shown, and the heart is the large organ shown in outline below the visceral clefts.

The double wall of the optic cup is shown in optic section as seen by transmitted light. The inner retinal layer is seen to be already thicker than the outer layer, which is destined to become the choroidal epithelium. The embryonic eyeball, or optic cup, is viewed in both cases from its outer or external aspect, and the choroid fissure is seen to interrupt the continuity of its ventral margin. Both layers of the cup are, however, seen to pass into or be continuous with each other on either side of the fissure. The eye, as a whole, is seen to lie in a rather ventral position with respect to the brain, so that that portion of the first cerebral vesicle, V_1 (Fig. 20), which is to form the future optic lobes—thalami—now projects high above the level of the top of the rudimentary eyeball. The olfactory pits, *ol*, have also been distinctly differentiated, as well as the rudiments, in Fig. 20, of the cerebral hemispheres, which are here just beginning to bud outward and upward. The vitreous humor is at this stage of considerable volume, as shown in

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the last figure by the space between the retinal wall of the optic cup and the lens in the centre. The vitreous humor of the eye, it may be remarked, soon becomes very much more voluminous in embryo birds than in embryo mammals of the same relative stage of development.

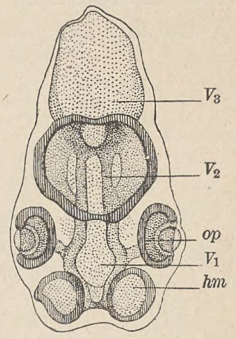
It is during the stages just referred to that the differentiation of the epithelial walls of the brain at different points begins to be very distinctly manifest. The sides of the walls of the future third ventricle (first embryonic vesicle) begin to thicken where the optic thalami are to be developed. A little farther backward the corpora bigemina (developed from the region marked V_2, Fig. 20) also begin to undergo a slight thickening ventrally and laterally. This region of the corpora bigemina (corpora quadrigemina of mammals) is very important in its relation to the development of the geniculate bodies and optic tract. While it cannot be said that the optic tract, the geniculate bodies, or the thalamus are yet definitely marked out, there is now an obvious tendency for the internal ganglionic layers in these regions to begin to be marked off from the pale external layer or mantle of axis-cylinder fibres. Farther back, in the region of the future fourth ventricle, V_3, there is a tendency for the dorsal epithelial wall of the neural tube to become quite thin, except at its extreme anterior portion, where the cerebellum is developed. Ventrally and laterally the walls of the third cerebral vesicle, V_3, are now rapidly thickening. This thickening is here associated, as in the more anterior parts of the brain, with the development of the ganglionic tracts internally, while the axis-cylinder fibres are developing externally. This gives to cross-sections through the walls of the nervous tube at this time the appearance of a more deeply stainable and opaque inner portion corresponding to the rudiments of the ganglionic tracts, while externally there is the appearance of a clear belt or zone that does not readily stain, that represents a delicate outer layer of neuroglia and the beginnings of the nerve-fibres, which have already grown outward from the more deeply embedded ganglionic or nerve cells, and have made their way longitudinally for some distance along the outer faces of the thalamus, pons, and medulla. Of the cord it may be said that in general the differentiation of the more deeply situated ganglionic tracts begins at its cephalic end and at the anterior or motor side. The white columns also begin to develop their anterior and lateral portions first, the posterior columns of white matter, or axis-cylinder fibres, appearing last of all. The relations of the pale outer and more deeply stainable inner layers of the brain are well shown in the walls of V_1 and V_2 of Fig. 46, representing a section through the head of an advanced embryo bird.

Some idea of the relations of the optic cups to the central nervous system in an embryo bird of the fourth day may be formed by reference to Fig. 21. Here the optic cups have been fully developed as such, and the whole head is seen from above, viewed as a transparent object. It is obvious from this figure that the changes in the form of the primary cavities of the brain since the end of the first day have been many and profound.

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The optic stalks have become quite narrow and slender. The lens has been separated from the overlying ectoderm for some time. The first primary cerebral vesicle, V_1, or what is left of it, may now be said to represent distinctly the rudiment of the third ventricle of human anatomy. It has also been much narrowed laterally, as the last figure shows. The hemispheres are now very distinct dorso-lateral outgrowths from the first embryonic cerebral vesicle, and both still have their simple epithelial walls. The second embryonic cerebral vesicle, V_2,—the future corpora bigemina,—has grown even more transversely than it has vertically, and there is now very obviously a spacious cavity within it, communicating anteriorly, through a narrow cleft, with V_1, and posteriorly, through an equally constricted passage,—the future aqueduct in part,—with V_3. The vesicle V_3 is now constricted anteriorly, but widens again abruptly and then slowly narrows, as the rudiment of the medulla, as it is continued backward into the spinal cord. The eyes, however, are still very prominent organs, and, while the adjacent parts of the brain have been expanding at a very rapid rate, the optic cups will soon begin to grow in the embryo bird at a disproportionately quick rate, so that they will soon become the most conspicuous and bulky organ of the head. The maximum volume of the eyes of embryo birds is reached about the ninth day of incubation, when their bulk almost or quite equals that of all the other organs of the head taken together. In this regard the embryos of birds differ very greatly from those of mammals. In mammals the eye of the embryo never reaches so disproportionately great a size, but remains small in comparison with the other parts of the head, especially as compared with the cerebral hemispheres. These latter soon overtop all the other organs of the head of the mammalian embryo in their rate of growth, since they very early become extremely massive, project upward and forward, and cause the peculiarly prominent and bullate form of the forehead of young fœtuses of the higher mammalia and the human species. In the fishes the maximum dimension of the eyes of the embryo is reached much earlier, proportionately, than in birds.

FIG. 21.



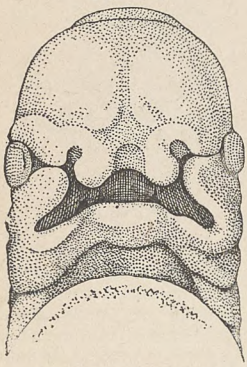
Head of an embryo chick 82 hours old, viewed from above.—*hm*, cerebral vesicles or hemispheres; V_1, first cerebral vesicle (= third ventricle); V_2, second cerebral vesicle; V_3, third cerebral vesicle (= fourth ventricle). Enlarged about 12 times. (After Duval.)

Up to the end of the fourth week the eye in the human embryo still occupies almost a lateral position, as seen in Fig. 22. The eye, in other words, is still looking laterally, as in fishes, and is not prospective or forward-looking, as in the adult. A blunt process, or downgrowth, from above the external nasal process separates the eye externally from the nasal fissure or pit, the rudiment of the nostril of the same side. Another process, or upgrowth, the maxillary process of the soft tissues below and in front of the eye, meets, but does not yet coalesce with, the external nasal process. The

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fissure thus left between the eye and the nasal opening of the embryo marks the course of the lacrymo-nasal groove, which remains apparent externally for a relatively long time. It is along the floor of this groove during the coalescence of its edges that the tear-duct is marked off and separated from the epiblast covering the groove. During the later transformations of the face the proximal or median end of the duct becomes more and more deeply involved by the surrounding tissues and down-growing margins of the external nostrils. This will be rendered obvious by an inspection of the figure just referred to, as well as of those that follow. The mouth as such is, relatively speaking, an enormous transverse cleft on the anterior side of the head during the fourth week. At two points on either side of the median line it communicates with the nasal pits or fossæ above, as shown in the figure. Should there be a failure to close of either or both of these clefts that connect the mouth and nose of the embryo at this stage, the deformity known as hare-lip would be the result.

FIG. 22.



Front view of head of a human embryo of 4 weeks. Enlarged 10 times. (After His.)—Showing the oral opening, joined on either side of the middle line by the nasal clefts above, and these laterally by the lacrymo-nasal grooves from the eyes, now lateral in position.

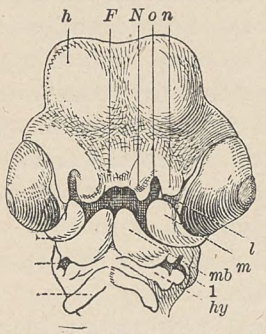
The cerebral hemispheres of the human embryo of the fourth week are seen to be very massive in proportion to the size of the eyes; much more so, in fact, than in the head of the bird embryo represented in Fig. 21. The forehead is already bullate and prominent, and a slight median depression indicates the position in which the future *falx cerebri* will be developed between the hemispheres. There is still no transverse, horizontal separation between the nasal and oral chambers. This is effected later by a median ingrowth from the roof and a pair of lateral ingrowths from the sides of the mouth at this stage, which finally meet in the middle line, thus not only separating the internal nasal from the permanent oral cavity, but also dividing the nasal chamber itself medially into its right and left halves. The face when viewed in profile is concave, with scarcely more than a beginning of an indication of the "nose," in the form of the fronto-nasal process lying between the two nasal pits and above the oral opening in Fig. 22. As we shall see in the succeeding figures, the "nose," so conspicuous a feature of the adult human profile, develops very gradually and very tardily by the growth forward and downward of the margins of the nasal pits, the tip of the nose being ultimately formed by the advancing apex of the fronto-nasal process, while the upper lip is formed partially by the downgrowth of the fronto-nasal process and partially by the coalescence of that process with the maxillary processes of either side.

The foregoing account of the early development of the eyes, head, and face of the human embryo may appropriately be supplemented with an account of the development of the corresponding parts of the em-

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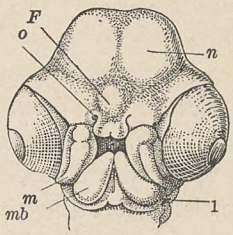
bryo of the bird. The parts corresponding in the bird to the nasal pits or fossæ are represented in Figs. 23, 24, 25, and 26. The very gradual steps by which the external nasal and maxillary processes fuse with the

FIG. 23.



Front of head of chick embryo of 6 days. Enlarged 6 times. (Reduced from Duval.)—*h*, cerebral hemisphere; *F*, fronto-nasal process; *N*, internal nasal process; *n*, external nasal process; *o*, olfactory, external nasal, opening; *l*, fissure along which the nasal duct develops; *m*, maxillary process; *mb*, mandibular process or arch; 1, auditory meatus; *hy*, hyoid arch.

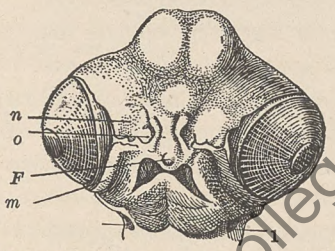
FIG. 24.



Front of head of chick embryo of 7 days. Enlarged 4½ times. (Reduced from Duval.)—*F*, fronto-nasal process; *n*, cerebral hemisphere; *o*, nasal opening; *m*, maxillary process; *mb*, mandibular process or arch; 1, auditory meatus.

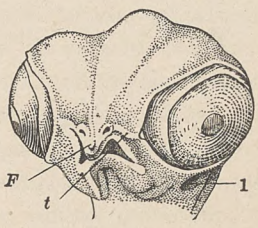
fronto-nasal process to form the upper beak of the bird, with the extension of all these and their convergence toward the median line, will be obvious from the mere inspection of the figures. These figures will serve to render still more impressive some of the other changes which have gone on in the development of the external eye and eyeball. The great and

FIG. 25.



Front view of head of 8-day chick embryo. Enlarged 4 times. (Reduced from Duval.)—*F*, fronto-nasal process, with egg-tooth rudiment appearing on its tip; *n*, external nasal process; *o*, external nasal opening; *m*, maxillary process, lacrymo-nasal groove still obvious, but eyelids more pronounced; 1, auditory meatus.

FIG. 26.



Front view, slightly oblique, of head of an embryo chick of 9 days. (Reduced from Duval.)—*F*, fronto-nasal process becoming pointed, with a suggestion of its future form, as the upper beak; *t*, ridge marking the position of line along which the nasal duct is formed; margins of eyelids and margin of third eyelid now very well differentiated; 1, auditory meatus.

rapid increase in the size of the eyeball, already noted, is one of the most striking changes which these figures illustrate. They also illustrate very clearly the fact that the optic cup of Figs. 17 and 21 is losing its cup-like character and may now be more properly spoken of as the *optic globe*

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or definitive eyeball; the edges of the optic cup have, in fact, been now deflected inward, while the cup itself has grown so greatly in size that the primitively wide opening into it on its outer aspect is reduced to a small round hole, the *pupil*. The edges of the optic cup now represent also the margin of the iris, of which we shall have more to say later.

The relatively great size of the eyes in the embryo bird during the stages represented by the last four figures gives to the head an appearance of inordinate width. The eyes are, in fact, now the most conspicuous organs in the whole head. They constitute the most conspicuous dilatation of the head in front of the neck. Just a little behind and below the eye, on each side of the head, the upper portion of the first visceral cleft, 1, remains open, as the external auditory meatus or external ear, but there is no considerable development of the margin of this opening, as in mammals, to form the pinna, or external ear.

The eyelids are already developing as slight folds around the equator of the optic globe, as shown in Figs. 23 and 24, but the third eyelid, or *membrana nictitans*, does not become a very conspicuous object until some time later, or about the ninth day, when, as in Fig. 26, it is conspicuous as a wide semilunar fold (*plica semilunaris*) within the outer eyelid proper, next the inner canthus. The eyelids proper, however, are not yet extended over the whole external face of the eyeball, and this does not happen in the embryo bird until near the middle of the third week of incubation. In Figs. 25 and 26 the course of the nasal or tear duct from the eye toward the nasal cavity can be distinctly traced from the inner canthus. The features which are distinctly diagnostic of the class of birds, so far as the appearance of the head and body is a guide, at the stage represented by Fig. 26, are the general form of the head, the obvious beak, the large eyes, and the incipient germs of feathers over some parts of the body. The nostrils already occupy their lateral positions near the base of the upper beak, and the position of the egg-tooth is indicated; the oral and nasal cavities are differentiated from each other. Figs. 23 and 24 also illustrate quite as clearly as Fig. 22 the relations of the first visceral arches, *mb*, to the development of the mandible, and of the maxillary processes, *m*, to the development of the maxillæ or upper maxillary region.

The preceding sketch of the earlier stages of the development of the face may be completed by a description of the appearances in profile of a series of human embryos ranging in age from the sixth to the eleventh week of intra-uterine development. Figs. 27 and 28 show the lacrymo-nasal groove extending from the eye to the outer border of the nasal opening along a line marked in the adult approximately by a line drawn from the inner canthus of the eye to a point on the outer posterior margin of the nostril next the upper lip and just within the ala, or thickened margin of the edge of the nostril where it joins the cheek. This line also in the adult lies approximately parallel with the tear or nasal duct, thus showing how nearly the involution of the ectoderm which gives rise in the

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embryo to the nasal or tear duct lies parallel or coincident with the line along which the lacrymo-nasal groove also closes in the embryo.

The nasal duct arises as a thickening of the under side of the epidermis along the line of the lacrymo-nasal groove. In man this differentiation begins about the end of the fifth or the beginning of the sixth week. The thickening forms a solid ridge, which then separates, except at each end, as a solid cord. This cord then acquires a lumen, or passage, within, so as to become a canal of epidermal (ectodermal) origin. The upper end of the originally solid cord expands at the inner canthus, preliminary to dividing into two branches which are to become the lacrymal canaliculi, that end at two small openings, the *puncta lacrymalia*, near the inner borders of the upper and lower lids respectively, just external to the *lacus*.

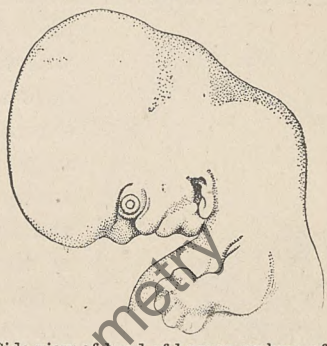
The external lacrymo-nasal groove itself ultimately disappears upon the approximation and coalescence of the juxtaposed edges of the external nasal, fronto-nasal, and maxillary processes. At a late stage no external

FIG. 27.



Side view of head of human embryo of 37 to 38 days and 14.5 millimetres long, to show the relations of the eye to the lacrymo-nasal groove. (Reduced from His's Atlas.)

FIG. 28.



Side view of head of human embryo of 39 to 40 days and 15.5 millimetres long, showing incipient eyelids appearing as faint folds above and below the eye. (Reduced from His's Atlas.)

traces of this are apparent in the Batrachia, Reptilia, Birds, and Mammals, but in Selachians part of what represents the continuation of this groove to the upper border of the mouth in mammalian embryos persists as a permanent fissure connecting the olfactory pit on each side with the upper border of the mouth.

The upper part of the face is bullate in all the remaining figures of the human embryo here given, owing to the great size of the overlying cerebral hemispheres. In Fig. 27, traces of the connection of the external auditory meatus with the remainder of the first visceral cleft are still visible. The head is strongly flexed upon the thorax, and the first indications of the digits and elbow are apparent. The eyes are still lateral in position. The nose is not yet prominent. The fourth ventricle is still a spacious and massive part of the central nervous system in proportion to the other portions, and there is a sharp bend at the point where in future the upper part of the neck will be situated. The profile is almost plane. The optic cup

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is in an advanced stage of development, so that the pupil is outlined. The inner and outer canthi are not yet marked out, however. In the next phase (Fig. 28), the first well-marked traces of the folds above and below the eye that are appearing are the rudiments of the future eyelids. The nose is here becoming just a little more prominent than in the foregoing figure, the forehead still more bullate, the head not so strongly flexed on the trunk, and the bend in the elbow still more marked. The eyes are also beginning to be turned so as to look obliquely forward; that is, the growth of the parts adjacent to the eyes is taking place in such a way that the eyes are being swung forward. The optic axes of both eyes would now converge if produced backward into the head.

The next three figures illustrate the further external changes that take place in the head of the human embryo up to the time of the closure of the eyelids and the consequent completion of the formation of the conjunctival sac. The method of the development of the lids has been already indicated in the account of the development of the bird. Here we shall have to describe the changes in the development of the eyelids more in detail. The plica semilunaris, or the feature representing the well-developed third eyelid of the advanced embryo of the bird, is very inconspicuous from an external inspection of the human embryo of the stages represented in Figs. 29, 30, and 31. The strong flexure of the head forward is disappearing, and there is only a strong convexity at the back of the neck where there was formerly a sharp bend. The brain, especially the cerebrum, has grown very greatly in volume, so that the face is becoming overhung by the forehead. The head, as a whole, is becoming globular, and is growing faster proportionally than the body. The edges of the external meatus of the ear are growing upward so as to form the beginnings of the pinna, or external ear, in the embryo represented in Fig. 29, while in Fig. 31 the form of the external ear is already fully outlined. The eyes do not yet look forward in Figs. 29 and 30, but obliquely outward and forward. The form of the eyes of the human fœtus, as viewed in profile at this time, reminds one very forcibly of the form of the eye as modelled by the ancient Egyptian sculptors in profile representations of the adult human figure on the walls of their temples. The course of the line of closure of the lacrymo-nasal groove is traceable in Fig. 29 when compared with Fig. 28. It appears that the inner canthus is slightly deflected toward the ala of the nose, and that the line from the apex of the inner canthus to the posterior part of the nasal opening marks the course of the line of closure of the

Fig. 29.

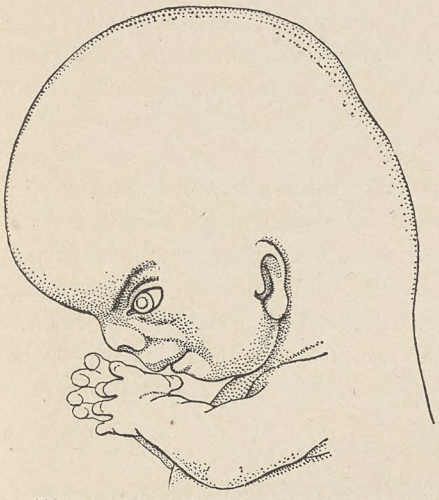


Side view of head of human embryo of 40–45 days and 16 millimetres long, showing the further differentiation of the pupil and eyelids beyond the condition shown in the preceding figure, and the appearance of the inner and outer canthi and closure externally of the lacrymo-nasal groove. (Reduced from His's Atlas.)

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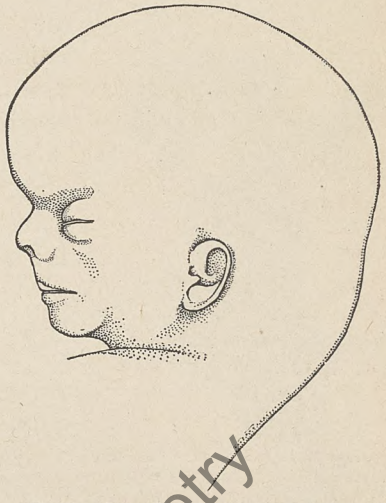
lacrymo-nasal groove, along which the nasal duct is included. The nose now becomes decidedly more prominent, and in Fig. 29 we begin to have an obviously human expression of countenance. While the upper and lower integumentary folds which are the first indications of the development of the eyelids have not yet converged internally or externally to form the canthi, such a convergence has occurred in the stage represented by Fig. 29. The inner canthus is still more definitely established in the stage represented in Fig. 30, and the upper end of the nasal duct has divided

FIG. 30.



Side view of head of human embryo of 58-62 days and 23 millimetres long, showing lids and canthi still more developed than in the preceding figure. (Reduced from His's Atlas.)

FIG. 31.



Profile view of head of human embryo 55 millimetres in length from cranial vertex to end of coccyx; age about 75 days. Enlarged about twice, to show the now closed lids and the thick, whitish superficial layer of epithelium, or epitrichium, between their edges, by means of which they adhere together. (Original.)

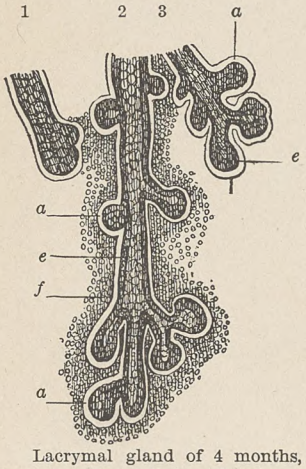
into the canaliculi of the upper and lower lids, which end in the adult at the puncta lacrymalia. The conjunctival sac has, however, not yet been completed, and this is not accomplished until the folds that are to form the upper and lower eyelids meet in front of the eyeball, as shown in Fig. 31. From the manner in which these folds grow over the eyeball, it is evident that the conjunctival sac is lined by the ectoderm. After the eyelids meet, as shown in the last figure, their edges coalesce, and remain so until shortly before birth. The epidermis of the inside of the lids, as well as that of their outer faces, is ectodermal, and the connective and muscular tissue interposed between the inner and outer ectodermal investment is mesodermal in origin. The orbicularis palpebræ muscle, in common with the superficial facial muscles generally, is derived from a thin sheet of superficial muscles which are represented in the neck by the platysma myoides, and on the trunk by the panniculus, or "fly-shakers," of many mammalia. The origin of the orbicularis palpebræ is probably to be traced

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to the blastema of the primitive myotomes or embryonic muscular segments of the upper part of the neck of the embryo.

The edges of the eyelids are seen to be fused together in Fig. 31, and a narrow light band of tissue seems to separate the edges of the upper and lower lids. This thin film of superficial ectoderm that cements the edges of the lids together is probably cast off when the lids separate, as a part of the general epitrichium of the body, at the time of birth. From the point of junction of the lids the eyelashes arise. These develop in the same way as hairs over other portions of skin, and they are entirely ectodermal in origin. Along the edges of the lids the Meibomian or sebaceous glands of the eye also arise during the fourth month as simple involutions of the ectoderm. The at first indifferent mesoderm of the eyelids becomes subdivided during the later stages into three structures: an outer or dermal layer, continuous with the dermis of the adjacent skin; an inner layer, continuous with the dermis, or connective tissue, of the conjunctiva proper, and perhaps with that of the cornea; and a middle layer, in which the muscular fibres of the palpebral muscle are developed.

FIG. 32.



Lacrymal gland of 4 months, human embryo. Enlarged 60 times. —1, young branch in the form of a solid cord of cells; 2 and 3, more advanced portions, with alveoli and canals appearing at centre; *e*, epithelium; *f*, connective-tissue sheaths of gland; *a*, still solid budding alveoli.

The lacrymal gland in man arises during the third month as a series of solid upgrowths of the ectoderm of the conjunctival sac into the mesoderm underlying the basal part of the upper eyelid. They arise near the outer canthus, under the upper lid. These outgrowths are at first solid, but soon acquire a lumen, and also send out diverticula, or branches, which are likewise at first solid. The tear-ducts of the lacrymal gland and their branches and the alveoli of the gland are therefore lined by cells that are derived from the ectoderm. The connective-tissue investment of the lacrymal gland, its ducts and follicles, and its blood-supply, are, of course, of mesodermal origin. Fig. 32 represents the lacrymal gland as figured by Kölliker from a four months' human fœtus, and illustrates very strikingly the manner in which racemose glands generally grow into and displace the surrounding mesoderm before them.

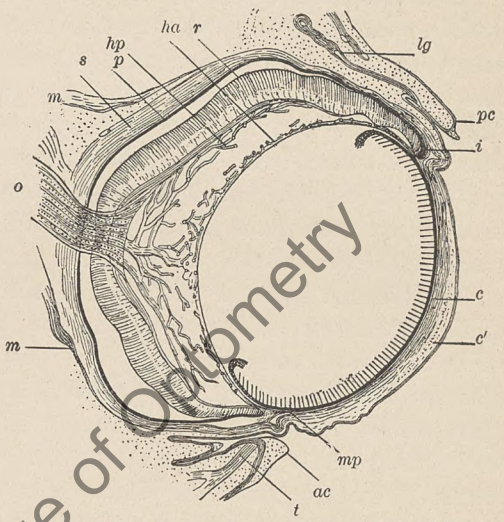
The lacus lacrymalis at the inner canthus of the eye is developed by the ninth week, but the caruncula lacrymalis develops considerably later. The glands of the caruncula are also of ectodermal origin, and are concerned in the production of the whitish secretion that accumulates at the inner angle of the eyelids. The diminutive glands of the caruncula are supposed to belong to the same series as the Meibomian, but it has been

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suggested by Giacomini that the caruncular glands in man represent the Harderian gland which opens at the inner canthus of the eye in other vertebrates. The development of the glands of the conjunctival sac varies greatly in different mammals; for example, the lacrymal gland of the common shrew-mole (*Blarina*) invests not only the whole embedded part of the diminutive and degenerate eyeball, but also its muscles, leaving only the corneal face exposed. The phylogenetic development of the glands that open into the conjunctival sac is not improbably to be associated with glandular structures that primarily opened upon the free surface of the ectoderm before the conjunctival sac was involuted in front of the eyeball in the course of the evolution of the eyelids. The eyelids, like other structures, have been gradually evolved in the higher types, since they are imperfectly developed in fishes.

The relations of the optic cup to the mesodermal envelope which covers it are well shown in Fig. 33, in a horizontal section of the eye of a mammalian embryo about one and one-fifth inches in length. This figure, in fact, illustrates the earlier relations of nearly all the structures that are found in the eye of the adult. The principal differences which it presents as compared with the fully-developed eye are the following: the imperfectly-developed lids, with their thickened margins of proliferated epidermis at *ac* and *pc*; the greatly-developed system of hyaloid vessels in the vitreous that arise from the arteria retinæ centralis; the axial vessel that extends temporarily through the vitreous along the future optic axis to the anterior hyaloid plexus; the disproportionate size of the lens, which still lies in contact with the cornea, under which there is still but little indication of the aqueous chamber; the thin and imperfectly-developed sclerotic and its vessels, as well as the still poorly developed lamina suprachoroidea.

FIG. 33.



Horizontal section of the eye of an embryo of the domestic ox, 3.5 centimetres long. Enlarged 20 times.—*ac*, anterior commissure of eyelid; *pc*, posterior commissure of same; *c'*, epithelium and superficial layers of corium of cornea; *c*, deeper connective tissue (corium) of cornea; *ha*, anterior plexus of hyaloid vessels in tunica vasculosa lentis; *hp*, posterior retinal hyaloid plexus; *i*, iris; *lg*, lacrymal gland; *m*, recti muscles; *mp*, membrana pupillaris; *o*, optic nerve, through which passes the arteria retinæ centralis, which sends a branch forward in the optic axis to join the anterior hyaloid plexus in the tunica vasculosa lentis; *p*, pigmented choroidal epithelium; *r*, retina; *s*, sclerotic; *t*, tear-duct; just beneath *ac*, in which *t* lies, may be noted a small fold, which is the third eyelid.

The retina is already beginning to differentiate into layers, while the

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cells of the outer or pigmented layer of the optic cup are now laden with pigmented granules. The retinal wall of the front portion of the optic cup is seen to be thinner than the posterior wall; the cup is, in fact, already beginning to show signs of differentiating into an anterior thin-walled uveal tract and a posterior thick-walled true retinal portion. The rudiments of the lacrymal gland have been laid down as a simple cylindrical proliferation from the conjunctival epithelium at *lg*. At the inner canthus the lacrymal canal at *t*, leading to the nasal duct, has already been formed, while just within the anterior commissure (*canthus*) at *ac* is seen a distinct fold completely covered by that portion of the eyelid represented by the commissure. This concealed fold represents the third eyelid or *plica semilunaris* of the adult. While the sclerotic is still thin, the muscles of the eyeball, the internal and external recti, are seen to be already attached to it by their distal tendinous portions.

The great proportional volume of the lens at this stage in comparison with that of the whole of the rest of the ocular globe is a striking feature of the development of the mammalian eye. The convexity of the cornea would appear to be at first directly determined by the convexity of the lens, since the cornea is now directly and closely superimposed upon the anterior surface of the latter. The subsequent and relatively more rapid distention of the portion of the optic globe enveloped by the sclerotic would seem to co-operate with the earlier mechanical relations above described that subsist between the lens and the cornea in giving to the eyeball its definitive and characteristic form, with its anterior corneal convexity greater than the convexity of any other part of its surface.

The vitreous space at this stage is still relatively inconsiderable, but, as Fig. 33 shows, it is traversed by two plexuses of vessels,—namely, a retinal net-work and a net-work over the posterior face of the lens. A vascular stem is continued straight forward from the central retinal artery, which traverses the distal part of the optic nerve or stalk, until it reaches the posterior face of the lens, where it branches into a fine capillary plexus. This artery is the capsular or anterior hyaloid artery, which passes forward through the hyaloid canal in the vitreous toward the lens.

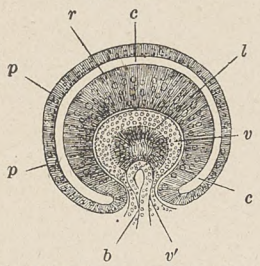
Before proceeding further, however, with our detailed description, we must recur to a consideration of the manner in which the vitreous is developed. We have already pointed out that the arteria centralis was an ingrowth into the continuation of the choroid fissure upon the under side of the optic stalk, as shown in Fig. 18. As a matter of fact, the whole blastema of the vitreous—namely, the delicate retiform tissue of which it is composed—is a product of the mesoderm, and is involuted into the optic cup at its inferior side through the choroid fissure. This involution begins during the fourth week of intra-uterine development, but the growth of the vitreous is not completed until much later. The first steps of the involution of the vitreous are represented in Figs. 34 and 35. The lens, *l*, in Fig. 34 is seen to be already invested by a distinct layer of tissue between its margin

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and the retina, *r*. This layer, which gives rise to the vascular tunic of the lens, or *tunica vasculosa lentis*, is a structure which provides in mammals for the embryonic growth of the lens, but undergoes complete atrophy long before adult life is reached. There exists no special means in the adult for the nutrition of the lens, for after attaining its full size the substance of the lens seems to manifest only a very feeble metabolism.

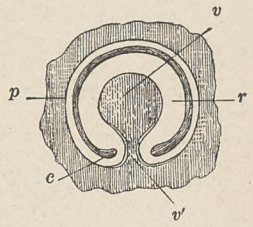
The tunica vasculosa lentis of the mammalian embryo is a highly vascular membrane which in its completed form envelops the lens on all sides, and in the human embryo is distinctly developed by the second month. Its vessels are derived, as already stated, from the capsular or anterior hyaloid

FIG. 34.



Anterior half of the eyeball of a human embryo of 4 weeks, in vertical section through its equator. Enlarged 66 times.—*l*, lens with central cavity; *v*, vitreous with its stalk, *v'*, passing through the choroid fissure; *b*, vascular loop that has been intruded into the fissure within the tissue of the vitreous; *r*, the retinal lamella of the secondary optic cup; *p*, *p*, outer lamella or choroidal epithelium of same; *c*, space between the two latter, representing the remains of the cavity of the primitive optic vesicle. (Reduced from Kölliker.)

FIG. 35.



The hinder half of the same eye as the preceding, viewed with reflected light. Enlarged 42 times.—*c*, cavity between pigmented layer, *p*, and retina, *r*; *v*, vitreous, and *v'*, points where the vitreous tissue is continuous through the choroid fissure with the mesoblastic tissue that invests the eye. (Reduced from Kölliker.)

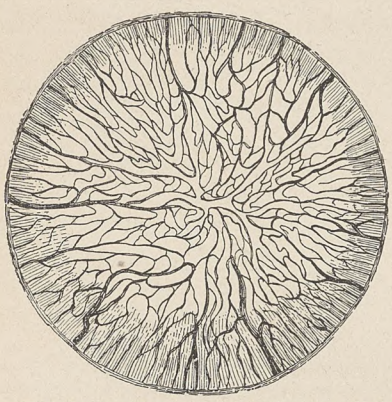
artery. This vessel, after reaching the lens, breaks up into radiating branches that spread out over the posterior face of the lens, ramifying through the mesodermal tissue of the tunic, as shown in Figs. 36 and 37. The mode of radiation and branching of these vessels on the posterior face of the lens is shown in Fig. 37. The branches upon reaching the equator or margin of the lens bend round over its front face and converge into a system of vascular loops, as shown in Fig. 36, traversing the anterior part of the tunica vasculosa lentis, or lens-capsule. These anterior loops of the vessels of the tunica vasculosa lentis also unite about this time around the margin of the lens with the vessels of the choroid which are now appearing. The tunica vasculosa lentis reaches its greatest development during the seventh month, after which it begins to degenerate, together with the capsular artery.

From the circumstance that the several parts of the nutritive membrane of the lens were discovered by different investigators at different times, these parts have received distinct names, such as membrana pupillaris, m. capsulo-pupillaris, and m. capsularis. The membrana pupillaris was first

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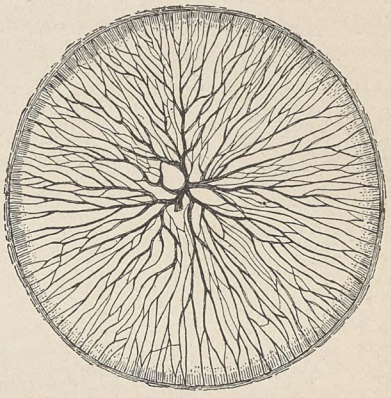
observed, perhaps, because it was situated under the pupil on the anterior face of the lens, and was therefore most easily found. Since it occasionally persists even after birth as a thin membrane closing the pupil, it may thus cause a congenital defect of the eye known as *atresia pupillæ congenita.* It has, however, been found that the membrana pupillaris is continued laterally from the pupil over the anterior face of the lens, this part receiving the name of membrana capsulo-pupillaris. Last of all, it was discovered that

FIG. 36.



Distribution of arteria hyaloidea on anterior wall of the capsule of the lens of a newly-born kitten. From an injection by Thiersch. (After Kölliker.)

FIG. 37.



Distribution of hyaloid artery on posterior wall of the capsule of the lens of a newly-born kitten. From an injection by Thiersch. (After Kölliker.)

this membrane was continuous, as illustrated above, Figs. 36 and 37, with the membrana capsularis on the posterior face of the lens. It is therefore needless to retain all these names, since they simply apply to parts of a single structure,—the membrana vasculosa lentis.

The other vessels of the eyeball which are external to the vitreous and retina are fully developed at a relatively later period. The ciliary arteries which penetrate the sclerotic a little distance from the entrance of the optic nerve are derived partly as an outgrowth from the same branch of the ophthalmic artery that gives rise to the arteria retinæ centralis. The vorticose veins do not reach their completed development till much later. The principal ramifications of the ciliary arteries and vasa vorticosa are within the lamina suprachoroidea, the first traces of which are laid down about the same time as the membrana vasculosa lentis.

The ciliary nerves which innervate the eyeball penetrate the sclerotic at first at about the same points posteriorly as the posterior ciliary arteries. They are centrifugal outgrowths from the ciliary ganglion, and their points of entrance through the sclerotic are arranged in a circle around and a little distance from the point of entrance of the optic nerve.

The nerve supplying the lacrymal gland is a centrifugal outgrowth of the ophthalmic branch of the fifth, or trigeminus. The blood-vessel, *the lacrymal artery*, supplying the lacrymal gland, is a comparatively late

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outgrowth of the ophthalmic artery, the capillary branches of which grow in between and around the developing follicles of the gland.

The vessels of the iris are outgrowths in part from the hyaloid plexus supplied by the *arteria retinæ centralis* and in part from the anterior ciliary arteries which pierce the sclerotic near the outer margin of the cornea, where they divide into two branches which grow toward each other and fuse along a circular course to form the great arterial circle of the iris.

The other surrounding mesodermal structures that may be further considered are especially the orbit, and the orbital muscles that control the movements of the ball. The latter, however, will require special consideration, but of the orbit it may be said that its conformation is largely due to the globular form of the optic cup itself. This is owing to the fact that the optic cup or foundation of the eyeball is formed before even the cranial cartilages and membranous matrices of the membrane-bones of the skull have been outlined. The result is that the surrounding hard parts must conform in a measure during their growth to the shape assumed by the previously-developed ocular cup or globe, as they develop partly in cartilage and partly in membrane.

DEVELOPMENT OF THE LENS.

The lens is developed, as we have already learned, from a circular patch of the epidermis (ectoderm) of the sides of the head of the embryo. As the primitive optic vesicles grow out from the anterior end of the medullary tube, their distal ends are pushed out against the ectoderm at the sides of the head. The circular area of the external ectoderm thus touched internally by the outer face of the optic vesicles begins to thicken and push itself inward. The outer or distal faces of the primitive optic vesicles at this time also become correspondingly depressed and concave externally. The appearance of the first traces of the secondary optic cup is therefore intimately associated with the growth and evolution of the lens. These changes occur quite early in the process of development: in the rabbit, for example, the involution of the lens begins on the eleventh day; in birds, still earlier, or by the end of the second day of incubation; in the human embryo, during the fourth week of intra-uterine life.

The thickening of the lens-rudiment is due to the growth or multiplication of the cells in the area of ectoderm from which the lens develops (see Fig. 16, *l*). The karyokinetic figures or nuclear spindles are said by Minot to be found in active division in the cells forming the outer face of the ectodermal rudiment of the lens during the eleventh day of its development. Nuclear spindles or cleavage-figures are also abundant, according to the same authority, on the inner face of the outer wall of the optic cup, which is also now rapidly thickening to form the future retina. This multiplication of the nuclei therefore proceeds, as pointed out by the same author, in homologous situations in both the ectodermal rudiments from which the lens and the retina respectively are destined to be developed.

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The pit-like involution of the ectoderm from which the lens is formed, as already stated, is intimately associated with a corresponding involution of the outer or distal and retinal wall of the primitive optic vesicle. In fact, this involution proceeds until the cavity between the outer or retinal wall and the inner or proximal wall—the future pigmented layer—of the optic vesicle is obliterated, and the latter is converted into a double-walled cup,—the secondary optic vesicle or cup. As the ectodermal involution destined to form the lens becomes deeper and more pit-like, the rim bounding the opening into the pit begins to constrict, and eventually closes. This pit-like involution is thus converted into a completely-closed sac or vesicle with cellular walls. When this closure has been completed, the ectodermal lens-vesicle, as we may now term it, detaches itself entirely from the immediately overlying epidermis at the point where the pit closed. At the same time the ectoderm (epidermis) immediately overlying the lens-vesicle also closes, so as to leave no trace of the opening that originally led from the exterior surface into the ectodermal lens-pit. In this way the ectoderm again becomes quite continuous over the underlying vesicular lens-rudiment. The ectoderm overlying the lens at this stage will eventually become the epidermis of the cornea.

It is clear from what has preceded that the future essentially refractive elements of the lens—that is, the cells of its body—are derived from the ectoderm. The lens-vesicle now occupies for a considerable time, in mammals, at least, the whole of the cavity of the secondary optic vesicle; that is, the lens now lies close against the future retina, as shown in Fig. 38, in which the rudiments of the membrana vasculosa lentis are also already visible. In the developing chick embryo (Fig. 15) a concavo-convex space begins to appear almost immediately between the proximal or retinal aspect of the lens-vesicle and the future retina. The space thus formed by the retreat of the retina from contact with the retinal aspect of the lens-vesicle in the eye of embryo birds is the vitreous chamber, and in them there is also for a long time no intrusion of blood-vessels into this space through the choroid fissure. In the embryos of mammals and man the lens-vesicle of this stage also at once begins to undergo histological differentiation, so that considerable progress is made toward a realization of its adult state before the retina begins to retreat to any marked extent from its retinal aspect. By the time the retreat of the retina from the posterior face of the lens-vesicle in mammals has begun, there has been pushed into the still very narrow concavo-convex space between the lens-vesicle and the retina a delicate, vascular, mesodermal membrane, the rudiment of the lens-capsule.

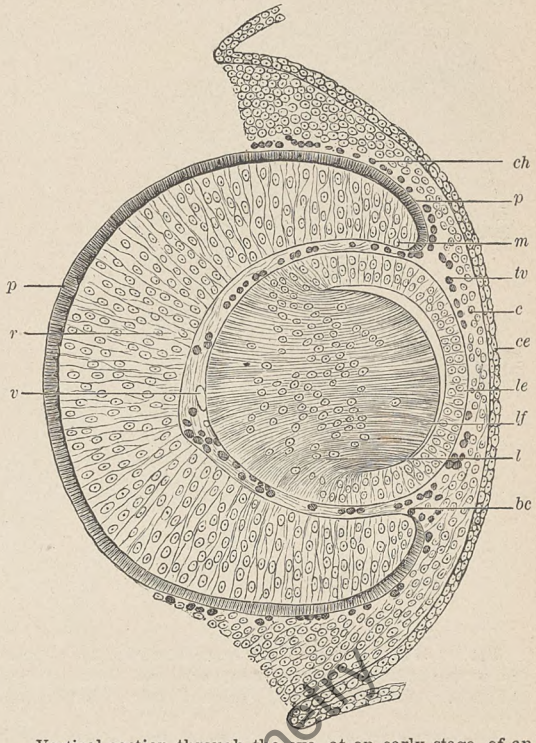
The lens-vesicle immediately after its involution is thick-walled, and may be said to close up the mouth of the optic cup, the rim of which is now bent inward all round toward the equator of the lens. The posterior wall is from the first slightly thicker at its middle than any other parts of the walls of the vesicle, and there is still a quite spacious cavity within it.

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In form, the lens-vesicle is now slightly flattened, and its exterior or corneal aspect is somewhat less convex than the posterior or retinal.

The subsequent changes in the anterior and posterior walls of the lens-vesicle are very different. The anterior wall (Fig. 38) becomes much thinner, and remains concavo-convex, while the posterior wall becomes very thick and bi-convex, so that the two walls are eventually perfectly coadapted and brought into contact with each other over their entire inner faces. From this cause it results that the original cavity within the lens-vesicle is at last completely obliterated. The obliteration of the lens-cavity is nearly complete in the stage represented in Fig. 38. This cavity is filled with fluid in the embryo of birds, but in mammals at the time of involution of the lens there is left a little superficial mass of loose cells (except in the mouse) at the bottom of the lens-pit. These cells seem to have been derived from the outer surface of the ectodermal area, which is involuted to form the lens. They are scattered in the cavity of the lens-vesicle of mammalian embryos, but are said to break down and disappear as the cavity of the lens vanishes, due to the thickening of its posterior wall, as described above. These free cells in the cavity of the lens-vesicle are suspected by Minot to be a part of the epitrichial layer of the ectodermal area which was involuted to form the lens.

FIG. 38.



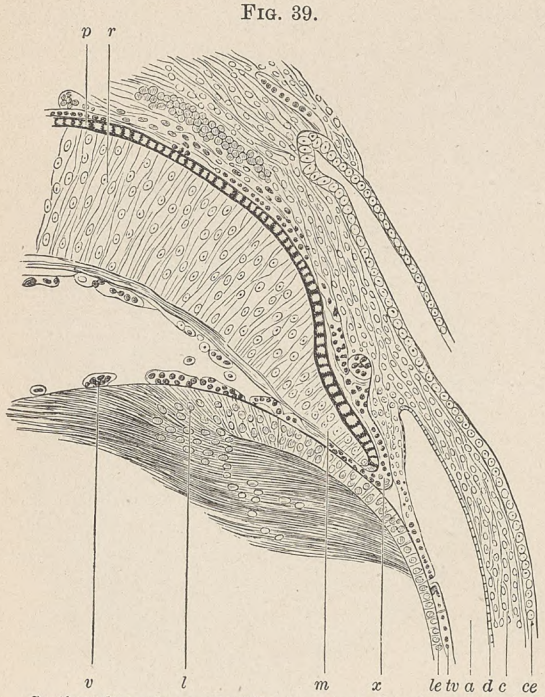
Vertical section through the eye, at an early stage, of an embryo mouse. Enlarged 130 times. (After Kessler, from Hertwig's Lehrbuch.)—*p*, pigmented epithelium, forming the outer layer of the secondary optic cup; *r*, thickened inner layer, the future retina; *m*, marginal zone, or border of secondary optic vesicle, which develops later into the non-sensory, ciliary, and iritic portions of the retina (uveal tract); *v*, vitreous body, with blood-vessels; *tv*, tunica vasculosa lentis; *bc*, blood-corpuscles; *ch*, choroid; *lf*, lens-fibres; *le*, anterior epithelium of lens; *l*, nuclear zone of lens-fibres; *c*, connective-tissue layer (corium) of cornea; *ce*, outer corneal epithelium.

The histological structure of the walls of the lens-vesicle is that of a columnar epithelium with the nuclei of adjacent cells lying at different levels in vertical sections. The posterior part of the wall of the lens-vesicle rapidly thickens; in fact, at the time of the closure of the vesicle this part

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of its wall is perceptibly thicker than the anterior portion. This is due to changes which go on simultaneously in both walls: while the cells of the posterior wall are becoming more elongated and columnar, the cells of the anterior wall are becoming converted into a thin epithelium composed of a single layer of cubical cells, as seen in Figs. 39 and 41. The cells of the posterior wall meanwhile become greatly elongated at the expense of their thickness, and are thus converted into the fibres of the later and more developed condition of the lens. During this process of elongation of the cells of the posterior wall of the lens, their nuclei, in a vertical section, as in Fig. 38, may be seen to extend as a scattered band across the middle of this wall from one edge of the organ to the other. A gradual transition of the elongated cells of the posterior wall of the lens to the epithelial cells of the anterior wall is effected all round the margin or equator of the organ, as shown at *l* in Fig. 39. During this elongation of the cells of the posterior wall they gradually undergo certain internal changes of constitution, as a consequence of which they acquire, as a whole, the transparency and refractive powers that characterize the fully-developed organ. The refractive properties of the lens are wholly due to properties acquired by the cells of the posterior wall of the lens-vesicle by the time its metamorphosis is completed. All the fibres extend from the front to the posterior face of the lens; those of the centre have a nearly straight course through its axis, while those outside the axis are more and more curved as the periphery of the lens is more nearly approached. Since all the fibres of the lens have blunt instead of

Fig. 39.



Section through a part of the lens and rim of the optic cup of a mouse embryo somewhat more advanced than that shown in Fig. 38. Enlarged 130 times. (From Hertwig's Lehrbuch, after Kessler.)

The section passes through the front of the lens, the margin of the optic cup, cornea, parts of aqueous and vitreous chambers, choroid and adjacent structures.—*p*, pigmented choroidal epithelium or outer layer of cup; *v*, blood-vessels of the vitreous body in the vascular capsule of the lens (the vessels cut through next the retina, *r*, represent the retinal plexus of the hyaloid artery); *m*, marginal zone of optic cup; *tv*, tunica vasculosa lentis; *x*, point of connection of the latter with the choroid; *l*, point of transition of anterior epithelial layer of cells of the lens into lens-fibres; *le*, anterior epithelium of lens; *a*, aqueous chamber of eye; *d*, Descemet's membrane; *c*, embryonic blastema of the clear corium of the cornea; *ce*, corneal epithelium.

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acute ends, they cannot converge at opposite poles of the optic axis of the organ. There is consequently developed a system of radiating lines of junction along which the ends of the successive layers of fibres are apposed. These so-called lens "stars" in the lens of the human adult have as many as nine rays, representing the lines of apposition of the ends of the lens-fibres of one face of the organ.

The growth of the lens is due to the apposition of new fibres, resulting from the division of the cells around the equator of the organ, just at the point where the anterior and posterior walls are continuous with each other, as at *l*, Fig. 39. Around the embryonic core represented by the original posterior embryonic wall of the lens-vesicle new lens-fibres thus arise. These new fibres are developed and arranged conformably with the curved surface of the lens, and at first extend from pole to pole of its axis, but later extend only from one of the radial lines of the posterior face to another nearly opposite radial line of the anterior face. These lines in newly-born mammals are triradiate, as represented in the annexed Fig. 40. These triradiate lines or "stars" of the embryonic lens alternate with one another, so that if the "star" of the anterior face were projected upon that of the posterior face the radii of the anterior "star" would exactly halve the angle between the rays of the posterior "star." In the adult, as already stated, the "stars" become more complicated, since "rays" or lines of juncture of lens-fibres are developed and intercalated in addition to those seen in the lens of the newly-born animal. This is due to the appositional mode of growth of the new fibres, which are laid down in layers over those that have been previously developed. It results from this fact that when the lens of an adult is macerated the fibres peel off in layers like the coats of an onion. The site of the production of the lens-fibres is around the margin of the lens, where nuclei in a condition of division are frequently seen during a late stage of the growth of the organ.

FIG. 40.

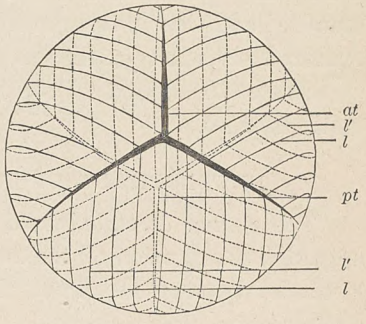


Diagram showing the arrangement and mode of convergence on the anterior and posterior aspects of the lens of a very young mammal of the fibres developed from the cells of its posterior wall. (Modified from Hertwig.)—*at* and *pt*, anterior and posterior triradiate figures or lines formed by the points of apposition of the anterior and posterior ends of the lens-fibres; *l*, *l*, lines indicating the direction of curvature of the fibres of the lens on its anterior face and their terminations along the triradiate line, *at*; *l'*, *l'*, continuation of the same fibres to the posterior triradiate line, *pt*. (Slightly modified from Hertwig's Lehrbuch.)

On account of the manner in which the lens-fibres are produced, it also results that an involution or pit is developed on the posterior or retinal aspect of the lens. The reason for this is to be sought in the mode in which the new fibres are produced around the equator of the organ. The ends of the newly-produced fibres extend backward and their posterior ends meet those of their fellows of the opposite side along a line which lies

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exactly in the optic axis of the organ. This pit or depression is very narrow, almost linear, in fact, as may be seen in the longitudinal section of the lens of a larval salamander, represented in Fig. 41, at *d'*. In the same figure the arched form of the zone of nuclei of the lens-fibres at *f* is also clearly indicated, so that the lens actually seems to have suffered involution of its posterior wall in the course of its development. This linear axial posterior involution is also apparent in the adult human lens, according to Babuchin, and is visible in sections through its axis.

The growth of the lens appears almost to cease toward the end of embryonic life. Huschke has shown that the lens has a weight of one hundred and twenty-three milligrammes in the newly-born child and of one hundred and ninety milligrammes in the adult. This shows that the total increase in the weight of the organ during adolescence is only sixty-seven milligrammes.

DEVELOPMENT OF THE RETINA AND OPTIC NERVE.

The retina, as stated in the introductory part of this article, may be regarded as a portion of the margin of the medullary plate which has been precociously separated from the latter and projected outward upon the hollow optic stalk. A study of the histological changes which it undergoes in the course of its development proves that this proceeds in a manner which is closely parallel to that of the development of the central nervous system, with the exception of the peculiar differentiation of its exterior layer of sensory cells that terminate in the so-called rods and cones.

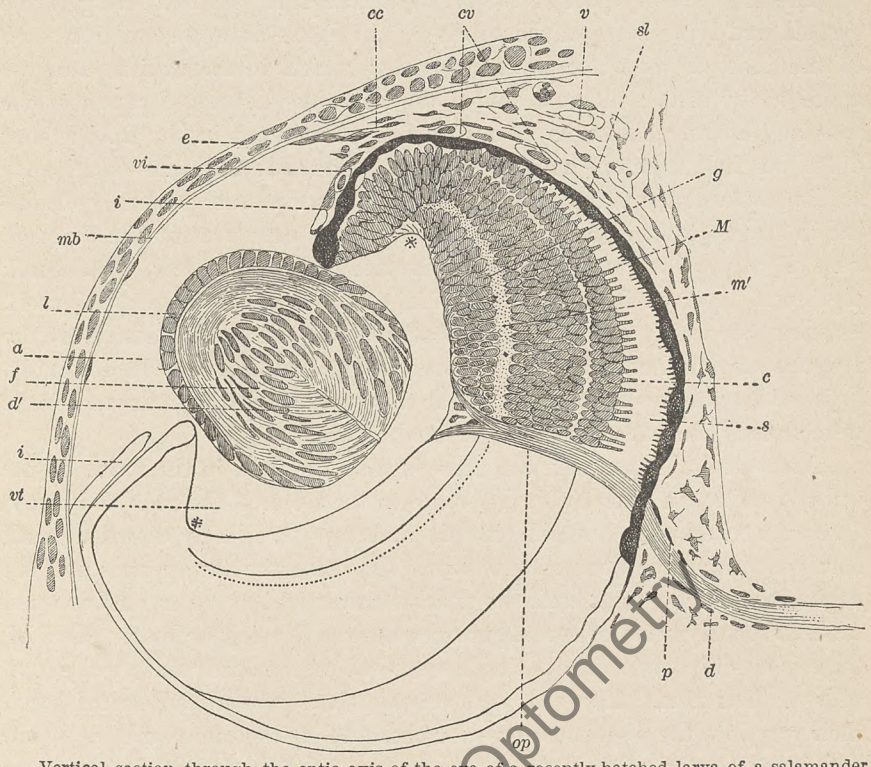
It appears that in the embryos of mammals, as in the cord and the brain, there is an early differentiation of the tissue of the retina into two zones,—an inner, non-cellular zone, and an outer, much thicker, nucleated cellular zone. This differentiation may be seen in the retina of an embryo rabbit from four to five millimetres in length, before there is any sign of the development of the rods and cones, or any indication of the splitting of the cells of the embryonic retina into strata. Minot regards the non-nucleated inner stratum of this stage as homologous with the non-nucleated stratum on the inner side of the developing spinal cord, and the thick outer nucleated layer as homologous with the internal neuroglia and ganglionic stratum of the developing wall of the spinal cord. The next step in the differentiation of the retina appears to be the subdivision of the wide outer nucleated zone into two layers of nearly equal thickness, distinguished by the appearance of their nuclei. The nuclei of the outer zone are smaller and tend to stain more deeply than those of the inner layer. This stage is observable in a rabbit embryo of twenty millimetres, or in a human embryo of thirty-eight millimetres. The outer layer is to be regarded as the rudiment of the true sensory epithelium of the retina, and gives rise to the rods and cones.

The inner layer of the embryonic retina, as described above, now undergoes differentiation into the inner reticular or molecular layer (Fig. 41, *M*)

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and the inner layer of ganglion-cells, *g*. The outer layer also undergoes differentiation into no fewer than three strata; the outermost of these is nucleated, gives rise on its surface to the rods and cones, and is separated by a thin reticular layer (*M*, Fig. 41) from a thick, inner nucleated layer.

FIG. 41.



Vertical section through the optic axis of the eye of a recently-hatched larva of a salamander (Amblystoma), 11 millimetres long.—*a*, space for aqueous humor; *c*, retinal rods and cones; *op*, optic nerve; *cc*, intruding corneal connective-tissue cells; *cv*, choroidal vessels; *d*, scattered cells of the disintegrating walls of the optic stalk; *d'*, pit in the posterior wall of the lens; *e*, epithelium of cornea; *f*, nuclei of fibres of posterior wall of lens; *g*, ganglionic or inner layer of retina; *i*, *i*, connective tissue of front of iris, with its vessels, *vi*; *l*, epithelium of anterior wall of lens; *M*, outer molecular layer; *m'*, inner molecular layer; *mb*, membrane of Bowman, with traces underneath it of endothelium of aqueous chamber; *p*, pigment-cells that have been developed from outer layer of optic stalk (the deeply-pigmented, black, and thick choroidal epithelium shows digitations on its inner face from which the cones of the retina have been withdrawn); *s*, space caused by shrinkage of retina away from choroid; *sl* points to a row of cells which mark the first traces of the sclerotic; *v*, vessel in the connective tissue investing the eye; *vt*, vitreous chamber; * * indicate the point external to which the uveal tract begins. (Original.)

This differentiation of the retina, however, does not extend over the whole of its area. As shown in Fig. 41, the true sensory area of the retina extends only between the two points marked * in the figure. Anterior to these the embryonic retina undergoes degenerative changes and becomes the foundation of the uveal tract, or *pars iridis retinæ*. The true retinal epithelium, in front of the points * *, finally becomes reduced to a single layer of cells closely adherent to the pigmented choroidal epithelium. It is also finally raised into longitudinal folds at short intervals about the

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points * *, and over that portion of its surface next the margin of the lens also is raised into annular ridges, or folds, that project all round toward the lens. This is the ciliary ridge, with its processes. The portion of the retina next the margin of the optic cup enters into, and forms part of, the posterior wall of the iris.

The true sensory part of the retina forming the posterior lining of the eyeball, and lying between the points * *, in Fig. 41, throws out from each of the cells of its outer layer a process which in batrachian embryos appears very early; the processes of the cells thus developed represent the rods and cones. These, as Babuchin has pointed out in the frog, at first differ but little from one another in form. The rods and cones (*c*, Fig. 41) are longest near the point of exit of the optic nerve, and gradually diminish in length toward the ciliary region, where they present the form of very slight papilliform elevations of the free ends of the cells. The black pigmented layer of the retina (choroidal epithelium) shows projections of its substance which were interposed between the rods and cones before the reagents used in hardening the embryo had pulled these two layers apart. It is evident, therefore, that in life at this early stage the rods and cones were already embedded in the pigmented layer.

According to Max Schultze, there is from the first, in the retina of the embryo chick, an appreciable difference in the form of the rods and cones. Over the membrana limitans externa there appear closely crowded small hemispherical projections of two sizes. Of these the larger ones are the beginnings of the cones, and the much smaller and more numerous ones, scattered evenly between the larger ones, are the developing rods. Each of these is an outgrowth from a single sense-cell of the outer sensory layer of cells of the retina. The rods and cones, as we have already noted, push their way into the pigmented layer or choroidal epithelium overlying them. The inner portion of the rods and cones develops first, and as the tips grow longer they form the external portions or outer segments. In the chick the development of the rods and cones begins on the seventh to the tenth day. In man and ruminants they are present at birth, though smaller than in the adult. The rods have been observed to begin their development in a human embryo of two hundred and fifteen millimetres.

There are two sets of cells developed in the retina, namely, nerve- or ganglion-cells and neuroglia-cells. The fibres of Müller belong to the latter class and develop very early, Herrick having found them in the eye of the salamander of about the same stage as that represented in Fig. 41. They extend from the internal to the external limiting membrane, these being clearly homologous in the retina with the same membranes developed on the inner and outer faces of the walls of the medullary canal or tube of the embryo. The ganglion-cells of the retina seem to be of two sorts,—namely, those which send processes from themselves into the molecular or reticular layers, and those which also send an axis-cylinder process into the optic nerve. Those which send axis-cylinder processes into the optic nerve

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compose the inner layer, *g*, Fig. 41. These, however, also send branched processes into the inner reticular layer, according to Dogiel and Cajal. The details regarding the development of the *amacrinal* cells of Ramón y Cajal, found in the middle layer, are not fully known.

The other layer which is concerned in sending branched processes into and over the reticular layers, thus forming a reticulum over the surfaces of these layers, is principally the middle layer of cells. The complexity of these nervous reticuli, formed by processes of the three layers of cells of the retina, is very great, as shown by Dogiel with the aid of the picrate of ammonia—methylene-blue—method. Herrick has shown that the middle layer sends processes into the inner reticular layer in the larval salamander. He has also shown that the ganglion-cells of the retina in all probability also originally arise upon what is morphologically the outer face of the retina; that is, the ganglionic cells originally proliferate from that face of the retina which ultimately bears the rods and cones. In this way it has been possible to co-ordinate completely the development of the ganglion-cells of the retina with that of the brain and cord, in both of which the ganglion-cells originally proliferate from near the surface of the inner wall of the medullary tube, or from that part of its surface which was exterior before the closure of the medullary groove.

The retina grows more rapidly in birds and mammals than its exterior envelope the sclerotic. From this cause it is thrown into folds, which project into the vitreous chamber. Kölliker states that the first fold arises below the point of exit of the optic nerve, and that numerous other radiating folds are added later. These folds gradually disappear toward the end of fœtal life, when the retina is smooth and lies for its whole extent closely in contact with the pigmented layer. Compare Figs. 19, 20, and 41.

The development of the special regions of the retina proper has been the subject of special investigation at the hands of Chiewitz, who has shown that the fovea or macula lutea is marked out very early as a region slightly thinner than the adjacent parts of the embryonic retina.

The blood-vessels of the retina, according to O. Schultze, are developed quite late. They appear in the pig of ninety millimetres, and in man after the third month. Over the surface of the retina, next the vitreous, a layer of cells is developed at this time. These cells arrange themselves into a net-work, from which blood-vessels are formed. The formation of vessels begins next the optic nerve, and radiates over the retina toward the margin of the lens. A layer of vessels is thus formed,—the membrana vasculosa retinæ. Red blood-corpuscles develop in this net-work, and in a fœtal pig of one hundred and seventy-five millimetres fine vessels were seen to have grown into the retina from this vascular membrane. This net-work is not supplied by the central artery of the retina, but probably by the short, posterior ciliary arteries. There are no blood-vessels developed in the layer of rods and cones, or in the outermost layer of the retina.

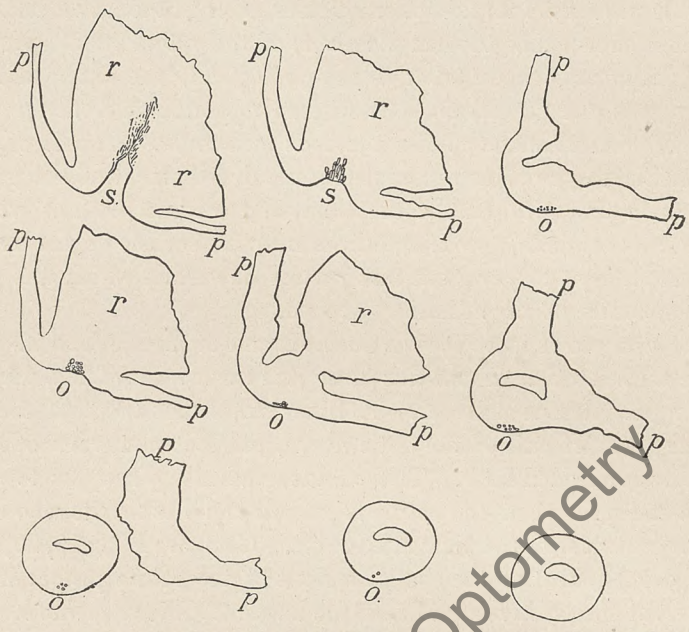
The lymphatics of the retina appear to develop and accompany the

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vessels as circumvascular spaces, as pointed out by His in respect to other parts of the lymphatic system of the eye and the vessels that traverse the nervous system.

The optic nerve seems at first to be formed solely of axis-cylinder processes from the ganglionic layer of the retina, which converge from every part of its internal functional surface toward the extreme median extremity of the choroid fissure of the eyeball, where they make their exit as a bundle of naked nerve-fibres. The mode in which these nerve-fibres arise

FIG. 42.



Series of figures from successive sections of the retina of an embryo torpedo near the point where the retina joins the optic stalk, *o*. The upper figures represent sections through the lower border of the retina and the proximal part of the choroid fissure. The axis-cylinder fibres, or nerve-fibres, of the retina are seen to be directed toward the roof of this fissure, *s*, and, as one passes to the sections in the lower part of the figure that cut through the optic stalk, it is evident that the nerve-fibres grow inward toward the brain between the cells of the lower wall of the stalk, as shown by the minute dots or circles. That this growth is at first entirely from the retina inward is proved by the fact that in the lowermost and last section of the optic stalk there are no fibres present in the lower wall. (After Froriep.)

is shown in Fig. 41. They pass through the retina and through the pigmented layer, a few cells of which are seen scattered along the course of the optic nerve at *p*. The optic nerve does not yet seem to have reached the brain; at least in my series of sections the connection could not be traced. A few scattered cells of the outer wall of the optic stalk are seen at *d*. From all this it is obvious that the optic stalk itself is not converted into the optic nerve.

The manner in which the optic-nerve fibres grow toward the brain from the retina is well illustrated by the accompanying series of sections

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copied from Froriep (Fig. 42), the significance of which can be fully appreciated from what has preceded, as well as from the subjoined summary of the investigations of Assheton.

In relation to the development of the optic nerve much difference of opinion formerly existed. Recent investigations, however, of which those of Müller, His, and Froriep were among the first, seem to have pretty firmly established the conclusion that the optic stalk takes a subordinate part in the development of the optic nerve, only, perhaps, directing the course of the growth of the axis-cylinder fibre of the optic nerve from the neuroblasts of the retina centrad and distad, or to and from the optic tract. Assheton has traced the development of the optic nerve in the frog, and reaches the following conclusions:

The optic stalk does not share in the formation of the nervous parts of the eye.

The optic stalk is broken down in the course of development, and the cells forming it are separated from one another, in part by the mechanical stretching due to the growth in thickness of the optic nerve, and in part by the growth of nerve-fibres between its component cells.

The optic nerve is developed independently of the optic stalk; its component nerve-fibres lie along the posterior border of the stalk, and at first entirely outside it, but on the breaking down of the stalk some of the nerve-fibres grow in between the cells of the latter.

The great majority of fibres forming the optic nerve arise as outgrowths from nerve-cells in the retina, and grow toward and into the brain.

According to Cajal's researches, certain fibres also exist which would seem to grow from the central nervous system to the retina, but these Assheton has not been able to find.

The nerve-fibres of the optic nerve pass over the ventral edge of the optic cup, and thereby cause the formation of the choroidal fissure.

The choroidal fissure of the embryo represents a condition in the evolution of the eye which was persistent in the adult prior to the evolution of the lens. Cajal also regards it as quite inaccurate to consider the fibres of the optic nerve as becoming connected with the elements of the inner or retinal wall of the cup after piercing the outer wall of pigmented choroidal epithelium, since the development shows that the fibres never really pierce either wall, but from the moment of their formation are on the outside of both. He also asserts that it is only by the subsequent growth of the rim of the optic cup that the bundle of nerve-fibres becomes surrounded by the walls of the cup, and so apparently pierces it. The choroidal fissure is, according to this author, due to an interference of the optic nerve-fibres with the growth of the ventral margin of the optic cup, as a result of which both its internal and its external wall are interrupted at this point. He also suggests that the choroidal fissure represents a stage in the evolution of the optic cup, that it was due to the eye having primitively a deep-seated origin from the cerebral wall, and that it subsequently grew toward

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the surface, as seems also to be indicated by what has been said in the first part of this article in reference to *Amphioxus*.

In chicks of four days, thick nerve-fibres may be found in the retina radiating toward and into the just-forming choroidal fissure, but can be traced no farther. In five-day chicks, the fibres are thinner, and can be easily traced into the choroidal fissure, but along the optic stalk near the brain there is no trace of nerve-fibres. In embryo chicks of six days, nerve-fibres can be traced all the way to the brain (Assheton).

Mihalkovics and Kölliker declare that fibres arise in the wall of the thalamencephalon and grow as a pair of bundles, following the optic tract toward the median ventral line from each side. Continuing to grow in their original directions, they at last cross each other, and each sends fibres into the optic nerve of the opposite side. Nerve-fibres thus also find their way centrifugally from the brain toward the retina, and at the point where these fibres cross the optic chiasma is developed. The complicated relations of the fibres within the chiasma remain to be more fully investigated. It appears to be rendered certain, by the investigations of Froriep and Assheton and myself, that the centripetal fibres are the first to be developed, at least in the lower vertebrates. That there are also centrifugal fibres developed at a later period seems equally certain. It is therefore exceedingly probable that the optic nerve in its fully-developed condition is formed of two sets of fibres, one of which is of centripetal or retinal origin, and the other of centrifugal or thalamic origin. But of these two the centrifugal seems to be developed at a later period than the centripetal or retinal set. The discussion of the development of the optic tract will be taken up later.

DEVELOPMENT OF THE SCLEROTIC AND CORNEA.

The first traces of the sclerotic in a just hatched salamander larva (Fig. 41, *sl*) are represented by a single layer of cells which can be traced from near the front of the optic cup, at this stage, to the point of exit of the optic nerve. The vessels of the choroid are beginning to appear at *cv*, Fig. 41 ; in fact, the mesoblastic rudiment, *i*, of the anterior stratum of the iris is beginning to become vascular at *vi*, in continuity with the vascular membrane associated with the development of the choroid. In front of the optic cup the cornea is represented externally by its epithelium, *e*, and internally by the basement-membrane of Bowman, *mb*, with traces of the epithelium of the anterior chamber. There is no canal of Schlemm yet developed, and the connective tissue of the cornea has but just begun to proliferate inward around the edge of the cornea, as at *cc*. There is no tunica vasculosa lentis developed. The sclerotic and cornea are present in their simplest forms, but the aqueous chamber, *a*, is already spacious, although not yet divided by the iris into a posterior and an anterior chamber.

While the sclerotic develops its numerous and interlaced fibres in the

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batrachian, with included connective-tissue cells, more tardily than in mammalia, some of the other parts are more precociously developed, as the aqueous chamber and the iris, for example, the foundations of which have been already in part laid down at the stage represented in Fig. 41. In a mammalian embryo proportionally but little more advanced than that from which the section of the eye just referred to was obtained, the sclerotic and cornea are far better developed. Comparing Fig. 33, the fibrous connective-tissue layer forming the sclerotic is already of considerable thickness, and serves for the attachment of the ocular muscles. The connective-tissue stratum, *c*, of the cornea that is continuous with the sclerotic has also grown under the epithelium, *c'*, and already forms a uniformly thick layer over the whole extent of the internal face of the corneal epithelium. In the chick, as early as the fourth day, the mesoderm grows inward around the edge of the corneal epithelium to form the connective-tissue layer of the cornea. In mammalia, the optic cup of the embryo (Fig. 38) is surrounded at a very early stage by mesoderm, which furnishes the connective-tissue cells between which the fibres of the sclerotic appear, as well as the basal substance and blastema of the corium of the cornea. In mammals, however, this mesodermal blastema in front of the optic cup soon divides into two layers, as shown in Fig. 39. One of these, *tv*, becomes the membrana pupillaris, and the other, *c*, the corium of the cornea, while a thin, adherent epithelial layer, *d*, becomes the endothelium of the aqueous chamber. In the cleft thus left between these layers of the mesodermal rudiments of the deeper layers of the cornea and the pupillary membrane, the aqueous humor appears.

The vascular layer on the external surface of the optic cup of mammalia develops at a very early stage, as shown in Fig. 38, *ch*. From it the choroid vessels and the lamina suprachoroidea are formed. In the lamina suprachoroidea scattered pigment-cells also appear external to the primary external pigmented or choroidal epithelium, *p*.

Underneath the sclerotic, in association with the choroid and the lamina suprachoroidea, an important lymph-space is developed. This space is, in fact, interposed between the lamina suprachoroidea and the inner face of the sclerotic. It is developed at first along the courses of the vessels, and communicates, by way of the passages of exit of the vasa vorticosa, with the lymphatic space of Tenon, which surrounds the eyeball as far forward as the edge of the cornea. The space of Tenon is bounded externally by the adipose and connective tissue, of mesodermal origin, of the orbit, in which the eye, optic nerve, muscles, nerves, and vessels are embedded. A lymph-space is also developed about the optic nerve within the space of Tenon and is separated from the latter by a delicate sheath surrounding the nerve. This space communicates with the arachnoid of the brain. These spaces complete their development comparatively late in the course of the growth of the embryo, though it is doubtless true that here, as elsewhere, the lymph-spaces appear very early around blood-vessels. Budge has shown

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that such lymph-spaces and vessels exist in the blastoderm of the chick of the second day of incubation. The canal of Schlemm, for example, has already appeared in the embryo pig of twenty-three millimetres as a passage that persists through adult life in the marginal mesoderm of the cornea.

VITREOUS HUMOR.

This, as already noted, is a mass of tissue of a peculiar, loose, transparent texture, which is intruded through the choroid fissure at the under side of the optic cup. In mammalian embryos blood-vessels accompany this intrusion to form the tunica vasculosa of the retina and lens. It is stated that mesodermal cells, in addition to those forming the walls of the vessels and their contained corpuscles, are found in the eyes of rabbit embryos of thirteen days. In the eyes of embryo birds there appears to be no intrusion of either cells or blood-vessels to form the vitreous humor, though in the eyes of embryo birds of the fourth day a non-nucleated reticulum may be seen in sections that represent a well-developed vitreous body. This vitreous reticulum seems to be entirely absent in the eye of the embryo salamander, Fig. 41.

The growth of the vitreous in the mammalian embryo probably takes place by the rapid development of a great quantity of its basal substance, or glassy matrix, with an absorption later of the mesodermal cells that were at first intruded. The hyaloid canal through its centre persists after the atrophy of the anterior hyaloid artery which supplies the vascular tunic of the lens. It is generally believed that this canal becomes a lymph-space.

A homogeneous layer—the hyaloid membrane—covers the surface of the vitreous at an early stage (on the fourth day in the chick). It lies in contact with the retina, the lens, and the ciliary processes. In the region of the ciliary body it becomes thickened and covers the ciliary processes. It here constitutes the suspensory ligament of the lens, or zonula Zinni, in which radiating fibres are developed that are attached to the capsule of the lens at its equator. Angelucci has found these fibres in chicks of the ninth day, and in embryos of the ox ninety millimetres in length. The capsule of the lens is a product of the membrana vasculosa lentis after the degeneration and disappearance of the vessels from the latter.

The imperfect closure of the choroid fissure during development results in a defective inferior border of the iris. Two pathological conditions result from an imperfect closure of the choroid fissure after the intrusion of the vitreous humor. If this closure is defective in the region of the choroid, *coloboma choroidea* results. If the defective closure extends to the edge of the optic cup where the iris is developed, *coloboma iridis* results. The lack of a uniform development of pigment-cells in the anterior mesodermal layer of the iris gives rise to a party-colored appearance of this organ, as a result of which some of the radii of the iris may appear much lighter in color than others. A change thus produced by defective development of pigment may affect any radius of the iris, whereas a congenital

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coloboma, due to the defective closure of the choroid fissure, can affect only some of its inferior radii.

THE IRIS, CILIARY PROCESSES, AND CILIARY MUSCLE.

These structures may very properly be considered together, since the courses of development of all these parts are very intimately associated. After the nearly complete investment of the optic cup by the sclerotic, and the coalescence of the fibrous mesodermal tissue of the latter (*co*, Fig. 42) with the corium (*c*) of the cornea, a complete connective-tissue envelope is formed, covering the essential structures of the eye that were of ectodermal origin. This process leads to the completion of the optic globe, or eyeball.

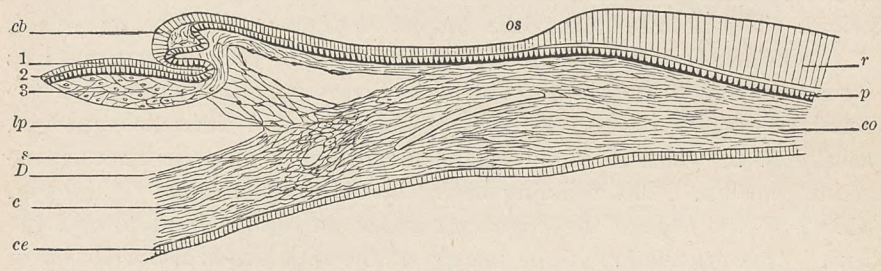
Coincidently with this process of investment of the optic cup and lens by a connective-tissue envelope, a series of very important changes in the relative thickness of the outer or marginal portion of the optic cup begin, as a result of which its edge becomes much thinner than the inner or true retinal portion. This thinning begins at the points marked * * in Fig. 41, where the edge of the optic cup makes an abrupt bend toward the lens. This attenuation of the margin of the optic cup is also well shown in Fig. 39 at *m*, and again, still more obviously, from the point marked *os* in Fig. 42. These points mark the boundary between the anterior or marginal zone of the optic cup and its true posterior retinal portion. This boundary is known as the *ora serrata* of anatomists, and in the embryo it marks the point from which the inner wall of the optic cup undergoes degenerative changes of such a character that its cells become transformed into a one-layered epithelium composed of cubical cells. This layer also lies closely in contact with the outer or pigmented layer of the cup. Meanwhile, the portion of the inner wall of the optic cup within the ora serrata (*r*, Fig. 42) remains thick and composed of several layers of cells, and becomes the retina. That is, the bottom of the cup remains as the retina, whereas its rim, or marginal portion, is associated with the development of the iris and ciliary body.

As the anterior marginal walls of the cup become attenuated they also extend more and more into the aqueous chamber between the lens and the cornea. This growth of the thin edges of the optic cup over the lens proceeds until it leaves only a small opening, the pupil, which leads into the optic cup. This thin marginal portion of the optic cup, overlying the lens, subsequently becomes incorporated into the iris. In newly-born mammals the eyes are blue; this is due to the reflection through the translucent outer mesodermal layer of the iris, 3, Fig. 43, of the color of the dark bluish-black pigment of the outer layer of the edge of the optic cup. The outer layer of the iris, 3, is split off from the mesoderm which forms the corium of the cornea at the time of the formation of the aqueous chamber, Fig. 39, *a*. Into this outer mesodermal layer of the iris amœboid pigment-cells proliferate after birth which are often of a different color from those that form the black epithelium of the outer cup or layer, 2, Fig. 43.

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In fact, these cells may be brown, yellow, greenish, or even brilliant red, as in the irides of some birds and reptiles. In man, these originally amœboid pigment-cells develop after birth, and probably migrate into the outer stratum of tissue of the iris, which is of mesodermal origin, from the choroid around the edge of the iris, or become pigmented *in situ* as cells of mesodermal origin. These cells of various tints of brown and black give the various tints of brown, hazel, and black that are seen in the iris of the human eye.

FIG. 43.



Section through the margin of the optic cup of an advanced embryo of a thrush of the second week of incubation (*Turdus musicus*). Enlarged 60 times. (After Kessler, from Hertwig's Lehrbuch.)—*r*, retina; *p*, pigmented outer layer or wall of cup; *co*, connective-tissue envelope of the optic cup, the thick sclera externally and choroid internally continued partly over the front of the iris and partly into the cornea, *c*, at the lower part of the figure; *os* indicates the position of the ora serrata or point where the retina is differentiated around the circumference of the globe of the eye into a posterior sensory and an anterior non-sensory epithelium; *cb*, ciliary body; 1, inner (retinal) and, 2, outer pigmented lamella of the pars iridis retinæ; 3, connective-tissue lamella of iris in which smooth muscular fibres, vessels, nerves, and pigment are developed; *lp*, pectinate ligament of iris; *s*, canal of Schlemm; *ce*, corneal epithelium.

This outer layer, 3, Fig. 43, of mesodermal origin, also gives rise to the stroma of the iris, as well as to its abundant non-striated muscles and blood-vessels. In mammals, Fig. 39, at *x*, this outer layer in the embryo is for a time continuous with the tunica vasculosa lentis anteriorly and the choroid posteriorly. This fact explains how the pupillary part of the vascular tunic of the lens for a time closes the pupil, and also why a failure to absorb this pupillary part of the vascular membrane leads to congenital *atresia pupillaris*.

The marginal portion of the optic cup external to the ora serrata begins to become attenuated in the eyes of the embryos of the domestic ox when they have reached a length of about one and one-fifth inch. In rabbit embryos this marginal thinning begins on the sixteenth day.

The portion of the optic cup which is immediately adjacent to the inner primary pigmented layer of the iris, and which surrounds the equator or margin of the lens, also belongs to the so-called marginal zone, and gradually undergoes elevation and plication, Fig. 43, *cb*. In connection with the adjacent layer of connective tissue outside this region, it is gradually transformed into the ciliary body. The inner aspect of the ciliary body is that of a cycle of meridional folds, which in man reach the number of seventy to eighty, the *corona ciliaris*, the free borders of which project toward the

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optic axis of the eye. There are also two or more annular folds apparent in the ciliary body in vertical sections of the eye, as shown in Fig. 42. The cycle of processes that arise together with the annular folds constitute the ciliary body of the adult. In a cat embryo ten millimetres in length these folds or ciliary processes are already well developed. Cross-sections of the folds in the eye of such an embryo show that but little connective tissue of mesodermal origin is carried into the spaces enclosed between the walls of the folds. The cause of the production of these folds is evidently to be ascribed to the more rapid growth of the area of the walls of the optic cup in the ciliary region than in the regions immediately behind and before it. The inner or retinal layer of these folds or ciliary processes remains unpigmented, whereas the outer layer is very strongly pigmented.

The ciliary processes gradually become very much thickened, and finally project inward and forward as rather blunt processes, owing to the increase in amount of the tissue of mesodermal origin within them which is proliferated from the outer rudiment of the choroid overlying them externally. The ciliary processes gradually acquire a firm union with the lens through the formation of the zonula Zinni, which in man is said to be formed during the fourth month. Some authors believe the zonula to arise from the vitreous body, and state that when the iris and the ciliary body are developed, the vitreous is traversed by fine fibres that extend from the ora serrata to the margin of the lens. It is asserted by Lieberkühn that the zonula is distinctly developed in eyes that have attained to half their full size.

The ciliary processes in man begin to appear in the human embryo about the end of the second or early in the third month. In the fifth month, Kölliker states, the processes are from 0.12 to 0.18 millimetre high and 0.10 to 0.12 millimetre wide. The mesoderm which grows into these processes from the outside becomes converted partly into the ciliary muscles and partly into the pectinate ligament, *lp*, Fig. 43. The proximal portion of the latter next to the ciliary body, *cb*, becomes the ligament, and the distal part, the muscle. The mesodermal rudiment which gives rise to the ciliary muscles and pectinate ligaments is originally continuous posteriorly with the choroidal layer, *ch*, Fig. 38, and anteriorly with the mesoderm of the iris, 3, Fig. 43. The rudiments of the ciliary muscles, both radiating and circular, seem to split off from the outer side of the embryonic rudiment of the choroid. It is asserted that in young birds of the last day of incubation the fibres of the ciliary muscle are transversely striated.

DEVELOPMENT OF THE THIRD, FOURTH, FIFTH, AND SIXTH NERVES.

The third, fourth, fifth, and sixth nerves and their associated ganglia comprise all the cranial pairs that concern the student of the evolution of the eye. In the lowest vertebrate known, *Amphioxus*, even when any of these nerves are developed, as the fifth, for example, they do not innervate any part of the eye, the latter having not yet been separated from the

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brain. In the lampreys and hags we first meet with these nerves developed in relation to the eyes.

Before proceeding further, however, it may be well to state that the cranial nerves that are related to the eye arise from nests or groups of ganglion-cells which bear a segmental relation to one another, especially in the region of the medulla oblongata. That is, there is embryological evidence which tends to show that some or all of these nests of ganglion-cells in the cord and brain are genetically related to the so-called somites or primitive segments of the head and upper cervical regions of the embryo long before the nerves themselves have developed. There are, in fact, serially recurring constrictions of the medullary tube in the head and body which correspond in number to that of the segmental rudiments of the muscles, or myotomes, which are, as is well known, parts of the so-called protovertebræ or embryonic segments of the embryo. These segmental differentiations of the medullary tube are visible even in the cephalic part of the embryonic neural system, especially in the medulla. From the fact that this segmental differentiation of the medullary tube divides the latter, in the embryo, into short, serially recurrent segments or regions transversely, the latter have been called neuromeres.

Along the dorsal median line where the medullary tube closes, the spinal ganglia, and certainly some of the cranial ganglia, are developed. This dorsal keel of the medullary tube, from which the ganglia of sensory roots of the spinal and some of the cranial nerves are developed, has been called the neural crest. This crest-like outgrowth of the medullary tube itself early shows a tendency toward segmental differentiation, as slight, serially recurrent thickenings, or knots of cells, which correspond to the neuromeres in number, and eventually give rise to the spinal ganglia and some of the cranial ganglia of the sensory roots of the nerve-pairs. These knots of cells grow outward and downward in pairs from the neural crest, so as eventually to push themselves into a lateral position alongside the medullary tube into the position of the ganglia of the sensory roots of the spinal and cranial nerves.

While the foregoing is in progress, the walls of the medullary tube, from which the brain and the spinal cord are formed, are also undergoing differentiation into regions lengthwise, marked off from one another by differences in the thickness of the wall and by four internal grooves,—a lateral one on each side, and a ventral and a dorsal one,—which traverse the inner surface of the medullary tube longitudinally. As a result of this differentiation, no fewer than six longitudinal bands or zones may be distinguished in a cross-section of the medullary tube or rudimentary cerebro-spinal axis of the vertebrate embryo. These longitudinal bands have been called by Minot the *zones and plates of His*, in honor of the distinguished German embryologist who first drew attention to them, and who has contributed so much to a thorough knowledge of the early development of the nervous system. There are six of these zones of His: two thin zones

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occupy a median position, one forming the dorsal and the other the ventral wall of the medullary tube; the four others form the most important portion of the lateral walls of the medullary tube, two on each side. The lateral zones are separated from each other by a groove or sulcus which extends from the foramina of Monro, at the anterior end of the medullary tube, backward over the lateral inner surface of the latter through the brain, as well as through the portion that is to be the spinal cord. The entire extent of the lateral walls of the medullary tube is thus divided by a pair of lateral grooves—the sulci of Monro—into a pair of dorsal and a pair of ventral longitudinal bands or zones. This demarcation of the lateral walls of the medullary tube into two zones may therefore be traced through the brain and the entire length of the spinal cord. The two lateral zones project somewhat into the cavity of the medullary tube on each side, so that the cavity in the tube—the future neural canal—is now somewhat lozenge-shaped, as seen in cross-section. These zones of the medullary tube are of such importance in leading to a correct understanding of the development of the central nervous system that the preceding account of their relations will not be considered superfluous.

The embryonic brain and cord being thus mapped out transversely into serially recurrent segments or neuromeres, and these again divided longitudinally by the sulci of Monro laterally and the thin dorsal and ventral plates dorsally and ventrally, six zones may be distinguished in each neuromere. The zones differ, however, in the extent of their development anteriorly and posteriorly. At the anterior part of the cord, or region of the medulla oblongata, the median dorsal plate becomes very wide and also very thin where it forms the roof of the fourth ventricle; for the remaining extent of the cord the dorsal plate remains narrow. The ventral plate on the under side of the cord remains narrow through the entire length of the embryonic nervous system, and becomes important as the portion through which the ventral or anterior commissural fibres pass from one side to the other through the entire length of the brain and the cord.

The lateral zones are the only ones that develop ganglion-cells. The dorsal zone, or that lying above the sulcus of Monro, is associated with the development of the dorsal or sensory roots of the spinal nerves, while the ventral zone, below the sulcus, is associated with the development of the motor roots of the spinal and cranial nerves. It may be added that the lateral or dorsal zones of His lie between the sulci of Monro, one on each side of the dorsal plate, while the ventral zones of His lie below the sulci of Monro, one on each side of the ventral plate. These preliminaries will enable us to follow intelligently the development of those cranial nerves, besides the optics, which are concerned in the innervation of the eye and its accessories.

In the wall of the medullary tube, along the zones of His, we finally have an epithelium of ectodermal origin, several cells deep. In the region of the dorsal and ventral plates and on the sides of the tube along the

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course of the sulci of Monro it is thinner than elsewhere. The first step in the differentiation of the cells composing the walls of the medullary tube is their separation into two sorts. One of these comprises the spongioblasts or young neuroglia-cells, called *spongioblasts* from the fact of their producing a reticular, fibrous, or spongy-looking supporting tissue (myelospongium, neuro-spongium) for the second sort,—the so-called *germinating cells*. The germinating cells undergo rapid division, and thus become the parents of the nerve-cells, or *neuroblasts*, which give rise to the axis-cylinder processes or nerve-fibres.

This multiplication of nerve-cells begins in the inner stratum, next the limitans interna, and between or among the embryonic neuroglia-cells, or spongioblasts. As the nerve-cells here multiply, the lateral zones of His increase in thickness. The neuroglia-cells extend from the inner side of the wall of the medullary tube to its outer side; their outer ends branch and anastomose with one another. The outer ends of the spongioblasts also soon form a spongy, non-nucleated, superficial reticulum which invests as a thin mantle (the so-called mantle-layer of neuroglia, or *Randschleier* of His) the rest of the tissues of the medullary wall. It is through and along this spongy *Randschleier* that the nerve-cells send out their axis-cylinder processes in the course of the development of the spinal and cranial nerves. The *Randschleier*, or mantle, is, in fact, the first indication of the appearance of the embryonic neuroglia which is to be traversed by the axis-cylinder fibres of the white columns and bundles, throughout the peduncles, medulla, and cord.

The neuroblasts or nerve-cells of the ventral zone of His throw out from the ventro-lateral face of the latter the anterior or motor roots as bundles of axis-cylinder fibres. These nerve-cells also send commissural fibres through the ventral or anterior plate across the median line. From the dorsal zone of His some axis-cylinder fibres emerge from its dorso-lateral face to join the sensory roots of the spinal nerves, so that the commissural fibres, the motor fibres of the anterior root, and some of the fibres of the dorsal root grow out centrifugally, or from nerve-cells that lie within the medullary tube. These nerve-cells also send axis-cylinder fibres lengthwise along the outer side of the cord through the *Randschleier* or primitive outer stratum of embryonic neuroglia investing the ganglionic tracts, the lateral zones of His.

The process of nerve-development is, however, very different with the ganglion-cells of the sensory ganglia. These contain nerve-cells which are bipolar. That is, each nerve-cell of a ganglion sends out two processes as axis-cylinders in two opposite directions, and therefore from opposite ends centrifugally and centripetally, or fibres are sent *from* the ganglion outward to the lateral parts of the embryo as well as *to* the central nervous system from the ganglion. In other words, one set of fibres grow out centrifugally from the outer or external ends of the cells in the same way as the nerve-cells of the anterior zone of His send out axis-cylinder fibres centrifugally

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to form the motor roots; another set, on the contrary, grow inward from the internally directed ends of the nerve-cells of the ganglion toward the cord and penetrate it along the course of the dorsal zone of His above the sulcus of Monro. Entering the cord, these fibres divide into anterior and posterior longitudinal branches which traverse the *Randschleier* and then give off *collateral branches* which subdivide and ramify in the gray matter.

A development of nerve-fibres may also proceed centrifugally from the extreme outer peripheral sense-cells, such as the retinal, olfactory, and auditory sensory epithelia, for example, and pass by way of the dorsal roots into the brain and medulla in the same way as the centripetal or ingrowing fibres from the nerve-cells of the sensory ganglia, but directly and without making any connections with the latter. If it be true, as appears very probable, that the optic nerve represents only a dorsal or sensory nerve the ganglionic foundation of which has been precociously separated and carried outward from the brain, we may possibly regard it as representative of the third type or method of development of nerve-fibres as described above. It is, however, very probable that the two types of the centripetal development of nerve-fibres here mentioned will be found to have been primitively the same as further embryological research clears up the many perplexing questions that still present themselves in connection with the development of the nervous system. There is, however, under all circumstances, a very broad distinction to be observed between *medullary* nerves that grow out directly as bundles of axis-cylinder fibres from groups of nerve-cells lying within the cerebro-spinal axis and those that may be regarded as *ganglionic* nerves, in which the nerve-fibres have grown into the cerebro-spinal axis from groups of nerve-cells lying external to the nervous system. We may now consider the development of the nerves that supply the muscles, etc., of the orbit, as well as the development and connections of the optic tract.

The Oculo-Motor or Third Nerve.—According to His, the third nerve grows out from the ventral zone in an inferior position, or, in anatomical language, from the under side of that region of the mid-brain which corresponds to the posterior quadrigeminal bodies or testes. A pair of clusters of nerve-cells or neuroblasts in the ventral zone send out an axis-cylinder process almost directly forward to the future ventral edge of the eyeball. It divides after reaching this point, and, as is well known, innervates five muscles,—rectus internus, rectus superior, rectus inferior, obliquus inferior, and levator palpebræ. Schwalbe discovered a ganglion belonging to this nerve in Selachians; the true ganglion of the oculo-motor of the mammalia has not yet been discovered in mammalian embryos, according to Minot. In mammalia it appears to be a purely medullary, and consequently a motor, nerve, as indicated by its development. It has been suspected by Minot that the transitory ganglion of the so-called thalamic nerve, discovered by Miss Platt in elasmobranchs, may represent the true ganglion of the oculo-

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motor nerve. The oculo-motor is distinctly developed in the human embryo of ten millimetres.

The Trochlearis, Patheticus, or Fourth Nerve.—This nerve has a most singular origin. It arises at the isthmus or on the dorsal side of the brain at the posterior limit of the posterior quadrigeminal body, immediately in front of the rudiment of the cerebellum. Its right and left trunks decussate at the point of exit from the mantle of neuroglia. It is quite well developed in a human embryo of ten millimetres or of the fifth week. This at first would appear to be a medullary nerve also, since the pair of groups of nerve-cells from which it arises are situated in the ventral zone of His. From these groups of nerve-cells a bundle of fibres passes upward on each side through the mantle layer of neuroglia within the medullary wall to their point of exit and decussation mentioned above. It has, however, been found that the peculiar course of the fibres is due to a migration downward of the neuroblasts within the wall of the medullary tube, and that the nerve of one side does not at first cross its fellow of the opposite side. The ganglion of the trochlearis was discovered in elasmobranchs by Froriep and Miss Platt; it appears to be for a time continuous with that of the trigeminal. The trochlearis in the human embryo passes straight forward toward the future superior side of the eyeball, across the course of the oculo-motor, and nearly parallel with the top of the head of an embryo two-fifths of an inch long, to join the superior oblique muscle, which it innervates.

The Trigeminal or Fifth Nerve.—This nerve, together with its Gasserian ganglion, is the most strongly developed of all the cranial nerves, its preponderating size and importance being apparent in all vertebrates at a very early stage. In man, its three branches—from which it derives its name of trigeminus—are already developed by the fifth week, together with the Gasserian and ciliary ganglia. Embryologically, as well as anatomically, this nerve proves to be of a mixed character; that is, its origin is a mixed one, since some of its fibres are of medullary and others of ganglionic origin, in conformity with its motor and sensory functions. The uppermost or ophthalmic branch, with its associated ciliary ganglia, is the principal one that concerns us. It is now known, however, that the development of the ciliary ganglion is intimately associated with that of the Gasserian, and that the former appears to be continuous with the latter at an early stage. In the lower vertebrates the ciliary ganglion is associated also with a single great trunk growing out centrifugally from the ganglion and known as the ramus ophthalmicus profundus. In man, however, the branches emanating directly from this ganglion are the ciliary nerves that pass to the eyeball, these being evidently centrifugal outgrowths from the ganglion. How the radix longa and radix brevis of the ciliary ganglion are developed in man is not known, but it is very probable that they are developed centrifugally. The frontal, nasal, and lacrymal branches of the ophthalmic are clearly in part at least centrifugal outgrowths from

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the Gasserian ganglion. The orbital and palpebral branches of the maxillary or second branch have a similar history.

The motor root of the trigeminal grows out from a pair of clusters of nerve-cells situated in the ventral zones of His, at the anterior end of the medulla oblongata of the embryo. The point of exit of the motor root is just below the level of the sulcus of Monro. The ascending sensory root penetrates the lateral wall of the medulla of the embryo from the Gasserian ganglion, just external to and above the sulcus of Monro, over the lower margin of the dorsal zone of His. The superior or first branch seems in the human embryo of the fifth week to be principally associated with the ciliary ganglion, and arises and passes almost vertically from the Gasserian ganglion to a position behind the eye.

The Abducens or Sixth Nerve.—This nerve is developed wholly from fibres that have grown out of the medulla oblongata centrifugally. It is therefore a medullary nerve. His discovered the nuclei of this nerve in the ventral zones that are called after him, situated pretty close to the median line or median ventral plate of the medulla oblongata. The points of exit of this pair of nerves in the embryo are already closer together and more decidedly ventral than those of any of the cranial pairs behind it. The ventral or motor root of the facial sends fibres into the ventral column of His which overarch the nuclei of the abducens. In the human embryo of the fifth week the sixth nerve passes almost vertically from the floor of the medulla upward toward the eye and at right angles to the fourth nerve.

DEVELOPMENT OF THE OPTIC TRACTS.

It would be superfluous here to discuss the gross anatomy and physiology of the optic tracts, but it has been thought best to preface the strictly embryological discussion of that region by briefly tracing the paths taken by the optic stimuli and the gross relations of the parts involved.

The path of the visual stimuli is from the sensory epithelium (the rods and cones) of the retina along the optic nerve to the chiasma. In the chiasma the fibres from the nasal or internal half of each retina cross to the optic tract of the opposite side. The optic tracts may be compared to a pair of flattened bundles of nerve-fibres which embrace the peduncles of the brain on each side from a point a little way behind the optic chiasma, somewhat as the reins of a bridle in the hands of a rider embrace the sides of the horse's neck. The optic tracts pass obliquely upward and backward on each side, and send fibres to the internal and external geniculate bodies, corpus subthalamicum, pulvinar, optic thalamus, and the upper side of the anterior quadrigeminal body; also through the anterior and posterior brachia of the quadrigeminal bodies, and by way of the latter and the optic tract itself to the internal capsule, along the optic radiation of the cerebral hemispheres to the visual cortex of the occipital lobes. It will therefore readily be understood that destruction or failure of develop-

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ment of the internal bundles of the optic tract must lead to the partial blindness known as hemianopia.

Experimentation in relation to the development of the optic tracts has yielded results of great interest and of some clinical value. Removal of the eyeball and section of the optic nerve result in degeneration of the optic tract. If the removal is carried out with a young animal, this centripetal degeneration of the nerve-fibres of the tract of one side is, however, not the only result, since it is found that the external geniculate body, the pulvinar, and the anterior quadrigeminal bodies do not undergo complete development. The trophic centre which controls the development of these deep-lying ganglionic parts in a young animal is therefore to be sought in the ganglionic cells of the retina, or in an extremely peripheral sense-organ. The retina, however, in spite of its extremely peripheral position, as shown by its development traced in the earlier part of this article, was primitively a part of the cerebral cortex which has been evaginated upon the optic stalk and greatly modified and specialized.

The converse experiment, namely, the extirpation or destruction of the temporal portion of the cerebral cortex in newly-born animals, leads to the imperfect development of the internal geniculate bodies and portions of the posterior corpora quadrigemina. A most interesting and promising field of investigation for students of the development of the eye has long since suggested itself to the writer,—namely, a study of the optic tracts of our common native American rodents, shrews and moles. I should expect to find, *a priori*, that in the shrews and moles these tracts would be very defectively developed, since their eyes are so minute—little over half a millimetre in diameter in the adult—that they can be of very little functional use. Here we might look for a defective development of the occipital visual cortex, the geniculate bodies, pulvinar, thalamus, etc. Here Nature has made the necessary preliminary experiment for us in almost extirpating the eye, and, inasmuch as these types also present us with one of the simplest forms of the mammalian brain, valuable results might be anticipated from such an investigation. Whether destruction of the occipital cortex in very young animals will produce degeneration of the geniculate bodies, pulvinar, and anterior quadrigeminal body does not seem to have been decided by experiment.

The following account of the development of the optic tract and its connections with the corpus subthalamicum, thalamus, pulvinar, geniculate bodies, and corpora quadrigemina is based upon the researches of Bernheimer, the illustrations to whose memoir have been reproduced here by photogravure process, but without the advantage of the colors of the originals. His results, as will be seen from the appended summary of his conclusions, have been got by tracing the development of the medullary sheaths of the nerve-fibres which traverse the intervals between the structures named. They are necessarily based upon sections of the region of the optic tract, the materials being for the most part derived from advanced

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FIG. 44.

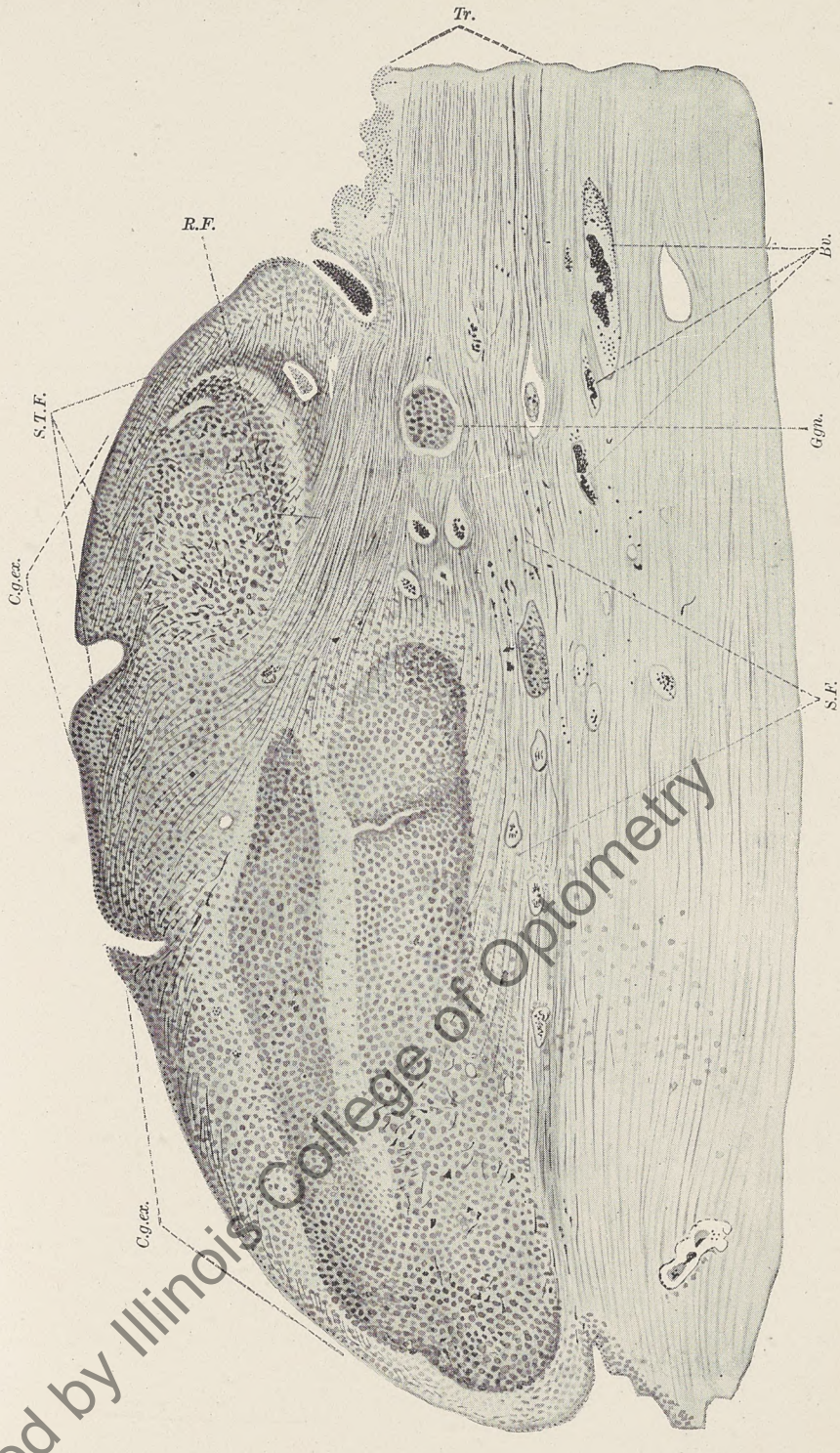
Oblique longitudinal section through the external geniculate body and base of optic tract of a human embryo of 36–38 weeks. Enlarged. (After Bernheimer.)

The upper free margin of the figure corresponds to the infero-external angle of the external geniculate body.—*S T.F.*, superficial tangential fibres and parts of fibres on the free outer border of the geniculate body; *R.F.*, radially arranged fibres, arising from a root composed of fan-shaped bundles; *S.F.*, superficially coursing fibres; *Ggn.*, ganglionic nidulus; *Bv.*, section through blood-vessels; *C.g.ex.*, corpus geniculatum externum; *Tr.*, tractus.

NOTE.—The piece from which the above section was cut was so embedded that the plane of section passed in a direction coincident with the long axis of the tractus and through the oblique long axis of the corpus geniculatum externum, in such a way, however, that the first section was cut off external to the outer surface of the external geniculate body; the following sections, therefore, subdivided the geniculate body from without inward and from above downward. The plane of section, in other words, converged anteriorly inward toward the median line, and also inward above toward the median line, and therefore departed somewhat, in a double sense, from a plane parallel to a true median one.

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FIG. 44.



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fœtuses. Figs. 44, 45, and 46 illustrate the development of the connections of the optic tract.

Investigation of the region of the outer geniculate body and optic tract in embryos, mature fœtuses, children, and adults shows that the fibres of the tractus have a double origin from the external geniculate body. First, fibres proceed from various points on the surface of the geniculate ganglion, mostly from above and below outward, pass thence from without inward obliquely, and radiate into the tractus as a whole, and after manifold decussation. Secondly, all the much more numerous remaining fibres arise from the inner layers of the external geniculate ganglion, in the form of a group of fan-shaped radiating bundles, and pass to the tractus in a somewhat oblique longitudinal plane. These fibres also pass from the external geniculate body to the beginning of the tractus in a slightly convergent direction. They are to be met with most distinctly within the geniculate body itself. These two sets of fibres show undoubted evidence of union with axis-cylinders and processes of ganglion-cells that decussate in every direction in the external geniculate body. Fibres that simply passed through the geniculate ganglion without ending within it could not be demonstrated. The external geniculate body is therefore to be regarded as the true ganglion of origin of a great part of the fibres of the tractus.

In embryos of from sixteen to twenty weeks, none of these fibres have yet developed their medullary sheaths. The first evidence of the development of the medullary sheaths is seen in embryos of from twenty to twenty-two weeks, in the form of delicate thickenings which extend for a greater or less distance along the fibres, though this is visible only in the fibres of deeper origin that arise in the form of the fan-shaped bundles. The fibres of superficial or external origin begin to develop their medullary sheaths after the twenty-eighth week of uterine existence, and after the deeper or first group of fibres has already developed a distinct, delicate, though by no means complete medullary investment. In fœtuses that are mature or nearly so, the medullary sheaths of both sets are completely developed, but they are still very thin, and the fibres appear distinctly isolated.

The same condition of affairs is seen in the brains of infants several weeks old; but in children several years old and in adults a change comes about, in consequence of the increase in the thickness of the medullary sheaths of the fibres causing the spaces between the individual fibres and bundles to become less evident. Single fibres can therefore no longer, in the late stages, be distinguished and traced to their sources of origin.

The optic tract receives a strong accession of fibres from the so-called corpus Luys or corpus subthalamicum. The larger part proceeds directly into the tractus after passing over the intermediate portion of the peduncles. The other portion takes a longer route, through, over, and around the internal geniculate body, to the tractus. Fibres also arise from the inner geniculate body, at the beginning of the tractus, with a so-called short root, without, however, radiating to the tractus in the form of bundles; these

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fibres originate and pass on singly to their destinations. The tractus also receives fibres that arise singly from the whole of the external surface of the internal geniculate body, with long or short roots, according as they originate farther from or nearer to the tractus.

From the thalamus fibres arise, as is already known, which may be distinguished as superficial and deep.

The deep root arises from the gray substance of the thalamus in the form of long and short fibres: the union of the fibres with ganglion-cells of the thalamus has been traced especially in respect to the latter; they pass below and between the geniculate bodies, and are best seen in the newly-born subject.

The superficial root of the thalamus arises from the ganglion-cells that are scattered in the cortical layers of the pulvinar (stratum zonale). They arise here and form a very dense and delicate plexus of fibres; fine fibrils of this plexus may be seen with axis-cylinder processes passing between the ganglion-cells.

Through this plexus fibres pass that do not join it. They may be distinctly traced to the tractus; but it cannot be definitely stated whence they originate. They do not arise from the basal ganglia; they are distinguished by their somewhat greater thickness and their more prolonged course. The development of their medullary sheaths is also characteristic. The supposition has been expressed that they are perhaps optic fibres that connect some of the cells of the retina directly with cells of the cortex, and they have been compared to the commissural fibres of the corpus callosum. Their physiological significance cannot be discussed here.

None of these fibres give evidence of a developed medullary sheath in embryos of the fourteenth to the sixteenth week. The development of medullary sheaths begins, as already stated, in embryos of from twenty to twenty-two weeks, most distinctly in the radiation from the corpus Luys or corpus subthalamicum, then in the fibres from the internal geniculate body and the deep root from the thalamus, and not at all in the fibres from the stratum zonale.

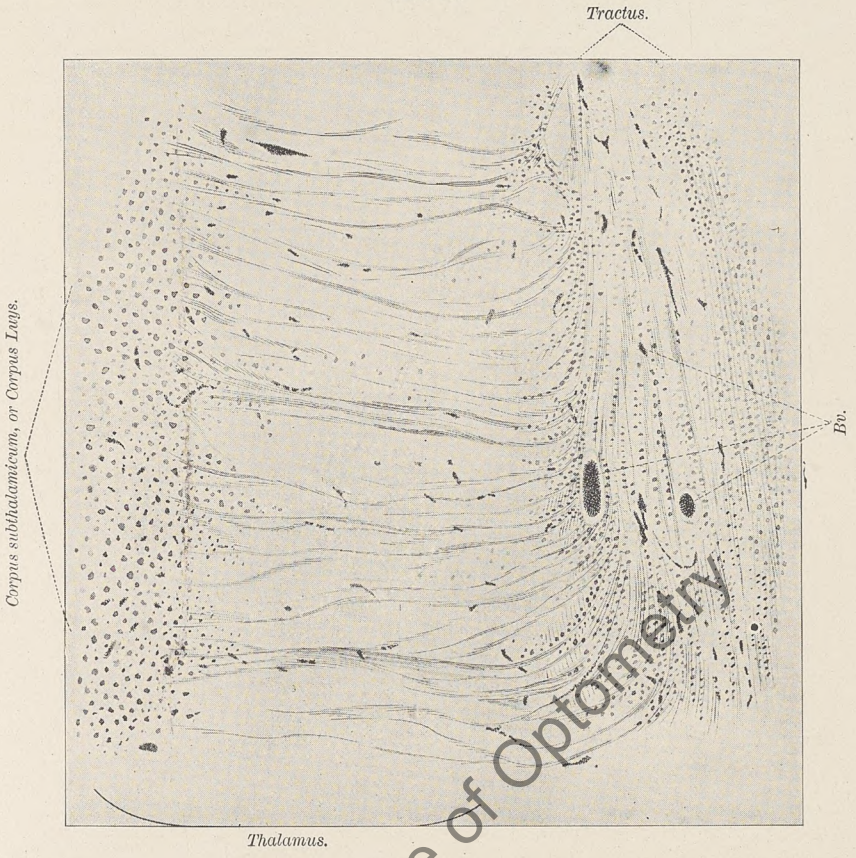
While all the bundles of fibres in embryos of the thirtieth week show the development of medullary sheaths, those proceeding from the stratum zonale are only beginning to develop sheaths. The so-called commissural fibres are not yet visible.

In embryos of the thirty-fourth to the thirty-sixth week the medullary sheaths of all the bundles of fibres just mentioned are apparent; those covering the fibres from the corpus subthalamicum are, however, the most distinctly developed. The superficial commissural fibres are not yet covered with a medullary sheath. These fibres are first distinctly developed in the brains of children several weeks old.

In the quadrigeminal region of the brain in embryos of from fourteen to sixteen weeks the nerve-fibres are still entirely without medullary sheaths. The first indications of medullary sheaths become apparent at the twentieth

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FIG. 45.



Horizontal section through the optic thalamus and deeper parts of the optic tract of a 34–36 weeks human embryo. (Enlarged, after Bernheimer.)

The section cuts through the optic thalamus, corpus subthalamicum (or corpus Luys), and tractus. The transverse bundles from the thalamus plainly converge toward the tractus. *Bv.*, sections through blood-vessels. The section passes in an almost horizontal plane, parallel to the longitudinal fibres of the tract, cutting the internal geniculate body tangentially, and so as to carry away a segment of the thalamus.

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to the twenty-second week, but exclusively in the region of the deeper bundles from the gray layer of both pairs of the corpora quadrigemina. Embryos of the thirtieth to the thirty-second week show a development of the medullary sheaths of the fibres of the stratum zonale for the first time. It would therefore seem that the appearance of the medullary sheaths of the deeper nerve-bundles that pass to the optic tract precedes that of the medullary sheaths of the more superficial bundles, on an average, by from four to eight weeks. By the thirty-fourth to the thirty-sixth week all the fibres from the quadrigeminal region have acquired medullary sheaths.

There can be no doubt that the corpora quadrigemina are far less important as centres of origin of optic fibres than are the ganglionic masses previously discussed. The importance of the corpora quadrigemina has been, in fact, as much overrated as the thalami and geniculate bodies have been underrated in this connection. The division into two bundles of the fibres that in the adult pass from the anterior pair of quadrigeminal bodies by way of the anterior brachium to the optic tract is not to be discovered in the brains of immature fœtuses or of recently-born children. It appears that not a very great many fibres can be traced as a radiation in part from the tractus to the surface of the anterior quadrigeminal bodies and in part to the deeper-lying gray substance of the latter. A superficial net-work of quadrigeminal fibres, forming a plexus somewhat similar to that seen at the posterior end of the thalamus (stratum zonale), could not be traced to ganglion-cells, nor could the centrifugal terminations of the fibres be satisfactorily made out. That these fibres pass into the optic tract cannot be stated as certain: all that can be said is that some of them converge toward the tract. Of the fibres that originate from the gray substance of the anterior quadrigeminal bodies some undoubtedly pass into the tract, though it may be said in a general way that, in comparison with those arising from the corpus subthalamicum (corpus Luys), the external geniculate body, and the deep root of the thalamus, they are very few in number.

The relations of the posterior quadrigeminal bodies to the optic tract appear to be somewhat similar to those of the anterior, and the fibres that pass from them to the optic tract seem to be few in number. There are probably fibres that pass by way of the posterior brachium over the internal geniculate body to the tractus.

It may be added here that the cerebral hemispheres are produced from the extreme anterior portion of the dorsal zone of His, so that the basal ganglion of the latter, the corpus striatum, may be said to originate above the sulcus of Monro. In the region of the mid-brain of the embryo the optic thalami are developed as thickenings of the dorsal zones of His. The thickenings that lead to the development of the thalami, and presumably to the development also of the pulvinar and corpus subthalamicum, are continuous anteriorly with the thickenings that develop into the corpora striata of the hemispheres. The sulci of Monro persist in the aqueduct or mid-brain, and it may be said that even in the adult the parts of the corpora quadri-

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gemina related to the innervation of the optic tract lie above those sulci. The probabilities are therefore greatly in favor of the view that the major portions of the ganglionic centres, here as elsewhere,—viz., the corpora quadrigemina and the geniculate bodies,—have also arisen in the embryo from the dorsal zone of His.

DEVELOPMENT OF THE MUSCLES OF THE EYEBALL, OR THE ORBITAL MUSCLES.

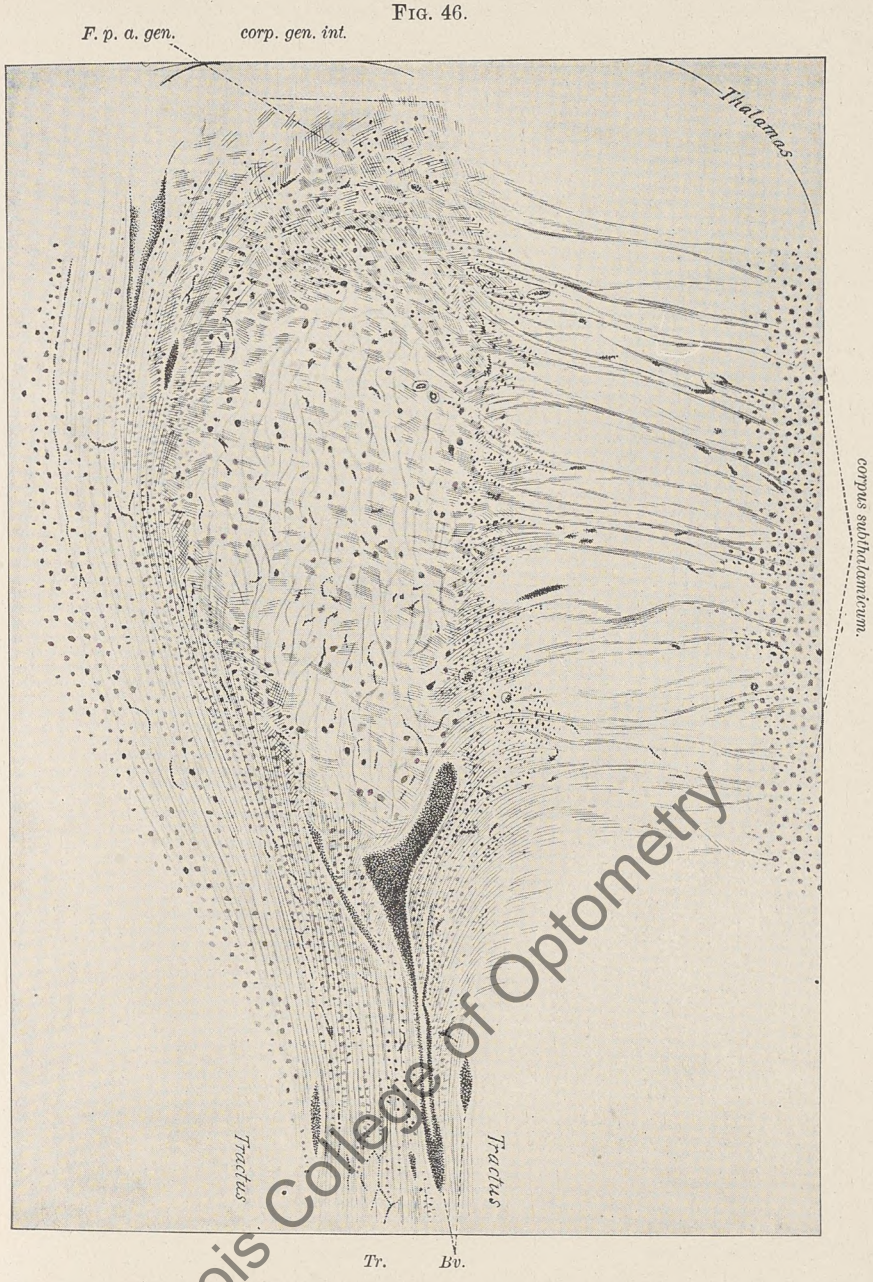
The development of the muscles that move the eyeball has not been genetically traced in the mammalian embryo. Since the acceptance of the doctrine of descent, it is, however, generally admitted that the less modified and abridged method of development of organs seen in the simpler fish-like vertebrates must be the primitive one. This primitive method of development in the lower forms often gives the clue to an understanding of the more complex and obscure processes of the embryonic growth of homologous parts in the higher types. Since the orbital muscles are homologous throughout almost all the classes of vertebrates, and since the primitive segments or somites of the embryos of vertebrates generally, from which they are derived, are serially homologous, I have not hesitated to utilize the knowledge gained in regard to the history of those muscles through a study of their development in the lower forms.

All the voluntary muscles of the trunk and limbs of vertebrates are genetically derived from the inner stratum of the so-called myotomes or muscle-plates that are parts of the paired blocks of mesoderm, sometimes called protovertebræ, well seen in the embryo bird of the second or the embryo rabbit of the eighth day. Embryological investigation has shown that the orbital muscles are no exception to this rule, and that, although it is difficult or perhaps impossible to trace such a genetic connection in the higher vertebrates, such a connection in all probability originally existed. Curiously enough, the representatives of the somites, muscle-plates, or myotomes of the head reach their fullest development only in the shark-like vertebrates, where they exist temporarily in the very young embryos, in which they were first discovered by Balfour and called by him the head-cavities. The cephalic myotomes from which the orbital muscles are known to be derived are parts of these head-cavities. The head-cavities are embedded in the indifferent mesoderm of the head, and undergo a most complex series of transformations in the course of the metamorphosis of portions of their walls into the orbital muscles.

The accompanying Fig. 47 will give a fairly good idea of the relations of the mesoderm of the head to the optic cup in an advanced stage of development in the bird. The optic nerve, II, is seen to pass from the base of the optic cup to the optic chiasma, crossing below the optic lobes and the infundibulum, *V*. Two dark bodies above and below the optic nerve represent portions of the orbital muscles, the recti, that have been cut through in place. Two nerves, the oculo-motor, *oc* and *n*, are also

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FIG. 46.



Horizontal section through the thalamus, inner geniculate body, and optic tract of a 34–36 weeks human embryo. (Enlarged, after Bernheimer.)

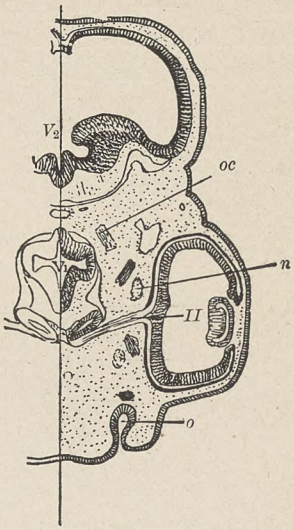
The section passes through the thalamus, corpus subthalamicum, internal geniculate body, and tract. It is nearly on the same plane as the preceding, Fig. 45, except that it cuts the thalamus at a point lower down.—*F. p. a. gen.*, fibres of the posterior angle of the internal geniculate body; *Bv.*, blood-vessels; *Tr.*, tractus.

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shown cut across. At the upper inner side of the optic cup a blood-vessel has been cut across. The important points to notice are the directions which these muscles and nerves are taking, and the fact that they are surrounded on all sides by an indifferent matrix of mesoderm with very few blood-vessels or lymph-spaces. In fact, at this stage of development in the chick, as well as in the mammalian embryo, there are as yet no capillaries. All the vessels now present represent in reality what are to become, generally speaking, much larger trunks; the permanent capillary circulation of the adult still remains to be developed. Into this mesodermal matrix the rudiments of the orbital muscles, nerves, and vessels grow and make their way at first as solid cellular processes or outgrowths. The discussion of the development of the orbital muscles may now be entered upon.

FIG. 47.



Transverse section through the head of a chick embryo at the end of the sixth day. Enlarged 11 times. (Reduced, from Duval.)—V_2, posterior part of corpora bigemina, or second cerebral vesicle, V_1, ventral and infundibular portion of first cerebral vesicle, from the ventral side of which the optic nerves, *II*, pass outward to the eye; *oc*, oculo-motor nerve, cut through obliquely; *n*, ophthalmic branch of fifth nerve (the darker oblong bodies represent oblique sections through the superior and inferior recti muscles); *o*, olfactory pit. The retina and the lens are formed, and a large vitreous space is now developed, but there are no vessels yet apparent in it.

It may be well, however, to note that the *retractor bulbi* muscle, so well developed in the lower mammalia (ungulates), is wanting in man. This hollow, conical muscle has not, moreover, been genetically traced to the "head-cavities," though it is not improbable that it, together with several other small intracranial muscles, may be found ultimately to have such a genetic history.

A very thorough study of the development of the muscles that move the eyeball has been carried out by Miss Julia B. Platt upon a shark (*Acanthias vulgaris*). These studies enable us to indicate at least what were the primitive conditions that attended the development of these muscles, though it is probable that the process has been greatly abbreviated and obscured in the case of the higher vertebrates, especially birds and mammals. In fact, in these forms no satisfactory studies of consecutive stages have yet been made.

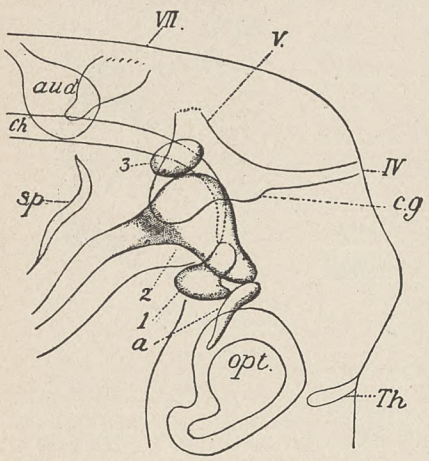
It appears from the work of the author cited that there are on either side of the head of the embryo of Acanthias four "head-cavities," as the spaces first discovered by Balfour in the heads of embryo sharks are called. These paired cavities unquestionably represent spaces within the head which are serially homologous with the mesodermal somites of the body farther back in the trunk of the embryo. They are structures that are evidently undergoing retrogressive development, since they do not persist to adult life as cavities, but undergo a complicated series of transformations which

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will be best understood by reference to the accompanying series of figures.

It appears that two (*a* and 1) of the four pairs of head-cavities in the embryos of sharks (Fig. 48) are premandibular in position. One pair—the third (2)—is closely associated with the mandible, and is spoken of as the mandibular cavity. The fourth pair (3) is behind the mandibular. The relations of these four structures can very easily be understood from the accompanying figures, which also elucidate the relations of these structures to the development of the muscles of the eyeball. These muscles are, in fact, differentiated from parts of the walls of these cavities, and in the course of this process the walls of the cavities are pushed out at definite points and in definite directions as prolongations, which are variously and appropriately bent about the eyeball toward its growing mesodermal coat (sclerotic), to which they eventually become affixed by their distal ends as a motor apparatus. In the very earliest stages of the development of these cavities they are present as four spaces on either side of the head, ranged somewhat in conformity with the curvature of the cranial flexure of the head of the embryo, and at first appear as globular or oval spaces, with no processes growing from their walls. The first of the cavities to throw out a process is cavity 2 of Fig. 49, or the mandibular. This process is extended backward and downward, and gives rise to a mandibular muscle which afterward degenerates.

Fig. 48.



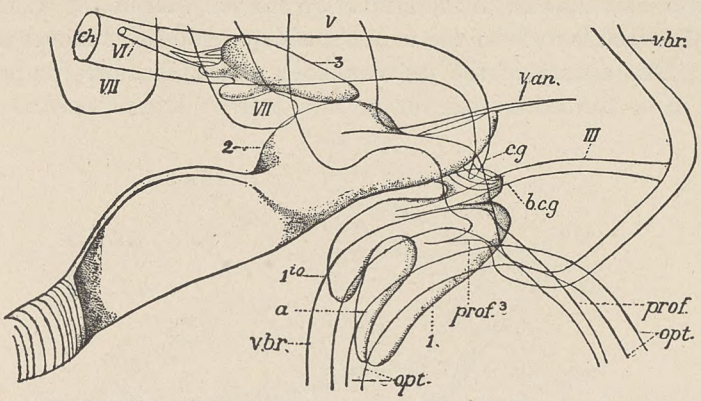
Side of part of head of an Acanthias embryo 6 millimetres long, showing the region of the cranial flexure as a transparent object, with the four head-cavities, *a*, 1, 2, 3, reconstructed from serial sections. These are shown in their primitive relation to the eye, *opt*, lying in a row behind and above the latter. *IV*, *V*, *VII*, cranial nerves; *Th*, thalamic nerve; *cg*, rudimentary ciliary ganglion; *ch*, anterior end of notochord; *aud*, auditory vesicle; *sp*, spiracular cleft. (Enlarged, after Miss Platt.)

The further steps by which the eye-muscles are evolved are illustrated by the remaining figures. It appears that the premandibular cavity, or that marked 1 in the figures, grows out into a concavo-convex plate somewhat conformably to the inner convexity of the eyeball. From it then arise as outgrowths four of the eye-muscles. These are the superior, inferior, and internal recti muscles, and the inferior oblique (see Figs. 50 and 51). The superior and internal recti arise from its anterior extremity, while the inferior rectus and inferior oblique arise as outgrowths from the postero-inferior angle of the cavity. From the third or mandibular cavity, marked 2 in the figures, and as an anterior outgrowth that bends toward the eyeball, the superior oblique muscle arises. From the fourth and last

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head-cavity, marked 3 in the figures, the external rectus is formed, about all of the blastema of this cavity being consumed in the development of

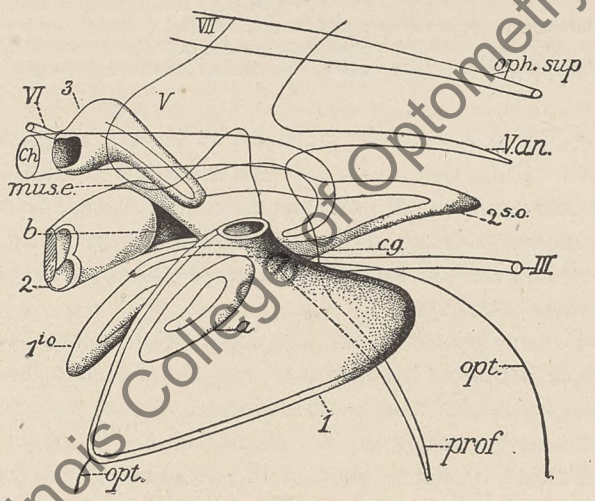
FIG. 49.



The four anterior head-cavities of an embryo of Acanthias 12 millimetres long, more advanced in their development than in the preceding figure.—*III* to *VII*, cranial nerves; *a*, 1, 2, 3, the head-cavities reconstructed; mandibular cavity 2 gives rise to a strong process extending backward, destined to form the transient mandibular muscle; 1^{io}, part of the premandibular head-cavity, 1, that gives rise to the inferior oblique muscle; *opt*, outline of upper part of eyeball; *prof*, ramus profundus ophthalmicus trigemini; *cg*, ciliary ganglion; *vbr*, floor of brain in region of cranial flexure; *ch*, anterior end of notochord; *Van*, branch from fifth, finally anastomosing with trochlearis; $prof^3$, branch from profundus opthalmicus toward anterior head-cavity. (Enlarged, after Miss Platt.)

this muscle. The rudimentary muscle developed as a backward extension of the mandibular cavity, close to the external rectus, afterward degener-

FIG. 50.



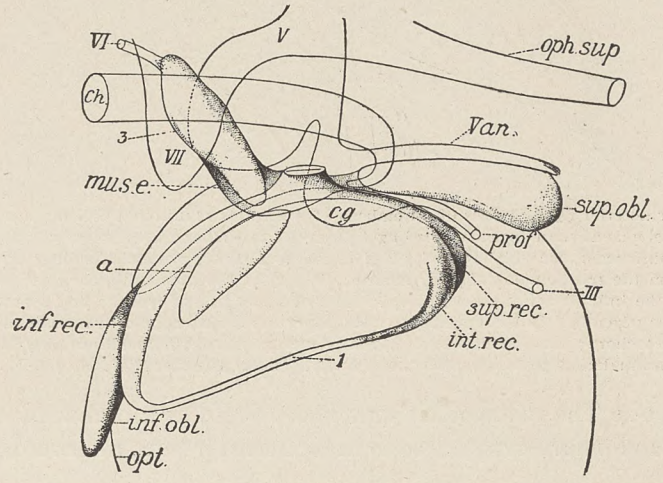
The four head-cavities of an embryo of Acanthias 16 millimetres long and advanced beyond the condition shown in the preceding figure. Only the anterior part of cavity 2 is now shown; mandibular cavity 2 is growing forward anteriorly at 2^{so} into the rudiment of the superior oblique muscle; premandibular cavity 1 is differentiating into the inferior oblique posteriorly at 1^{io}. Other letters as before. *Oph. sup.*, superior ophthalmic branch of seventh cranial nerve. (Enlarged, after Miss Platt.)

ates, and is lost in indifferent mesoderm. The first cavity, or that marked *a* in the figures, also appears to degenerate into indifferent mesoderm.

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Miss Platt's studies also disclosed the following facts. The muscle-cells of the external rectus first appear in the median wall of cavity 3, and they pass from this wall into the cavity, ultimately filling it. The muscular tissue also first appears in the median or internal wall of the mandibular cavity (2) which is to form the superior oblique and the rudimentary jaw muscle. The history of the premandibular cavity is more complex. It appears to be formed by the fusion of a pair of lateral cavities with a

FIG. 51.



Still more advanced condition of the head-cavities of an embryo of Acanthias, from the side, as before.—Premandibular cavity 1 is giving rise to the rudiments of the inferior oblique, *inf. obl.*; inferior, superior, and internal recti, *inf. rec.*, *sup. rec.*, and *int. rec.*; mandibular cavity 2 is showing the extension of the superior oblique, *sup. obl.*, still more prominently than in the preceding figure; cavity 3 is extending as the rudiment of the external rectus. Other letters as before. (Enlarged, after Miss Platt.)

median space, which is generally supposed to have a morphological value widely different from that of the two cavities which it unites. The four premandibular eye-muscles are said by Miss Platt to arise from the dorsal wall of the lateral portions of the premandibular cavity, approximating closely, in their place of origin, the line of fusion between the paired cavities and the central space.

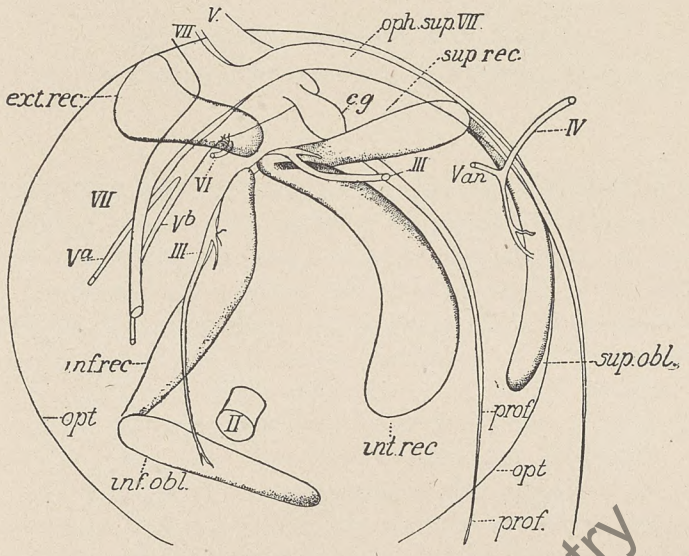
The transformations attending the innervation of the external rectus by the sixth or abducens nerve can be very satisfactorily traced from the accompanying figures, as well as the manner in which the relations of the third or oculo-motor nerve to the inferior rectus, inferior oblique, and superior rectus are brought about in the progress of development. The development of the relations of the fourth or trochlearis to the superior oblique muscle is also shown, as well as its mode of anastomosis with the trigeminus or fifth nerve at *Van.* It also appears that the trochlearis and the trigeminus have at first a common origin, but soon become divided.

These figures, including the last, Fig. 52, enable one to trace very satis-

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factorily the history of essentially important orbital muscles, which, as will be seen from the last stage represented, present a strong analogy to those of the human subject in their mode of arrangement. The wonderful manner in which these outgrowths from the head-cavities grope their way through the mesoderm and embrace the eyeball, seeking, so to speak, for their proper points of insertion upon it, as shown in Fig. 51, is, to say the least, a most

FIG. 52.



The transformation of the head-cavities nearly completed in an embryo of Acanthias 55 millimetres long.—Cavity 1 has given rise to inferior oblique, inferior rectus, interior and superior recti; cavity 2 has given rise to superior oblique, and cavity 3 to external rectus. The mode in which the innervation of these muscles is achieved by *III*, *IV*, and *VI*, pairs of cranial nerves, is also shown. The eyeball, *opt*, is supposed to be transparent, and all the foregoing structures lie behind or beneath it. *II* indicates the position of the point of union of the optic nerve with the eyeball. (Enlarged, after Miss Platt.)

remarkable fact. How these parts, as well as all others in the embryo, are guided to grow to just the right proportions in respect to one another, how they are guided in the course of their extension through its mesodermal tissues to exactly the right places, must ever remain an unsolved problem. We may say that the hereditary tendencies of the germinal matter of the embryo determine these processes, and that this germinal matter is transmitted as an actual, visible substance from generation to generation continuously. This manner of disposing of the questions raised is, however, unsatisfactory, since it is not really an explanation. It is too general a statement. When it is attempted to particularize, as has recently been done by an eminent biologist, we become hopelessly involved in a maze of speculation.

The development of the muscles of the face, including the orbicularis, has been traced by Ruge to the platysma myoides (musculus subcutaneus colli), which is to be regarded as a part of a muscle which in the ancestors

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of mammals extended forward from the neck over the face, where the whole have been innervated by the facial or seventh nerve. Nothing is known of the development of the tensor tarsi (Horner's muscle) at the inner angle of the orbit. This muscle, in common with the orbicularis palpebrarum, corrugator supercilii, etc., is innervated by the facialis, and its development must therefore be associated with that nerve and the platysma myoides muscle.

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THE ANATOMY OF THE ORBIT AND THE APPENDAGES OF THE EYE.

BY THOMAS DWIGHT, M.D., LL.D.,

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THE following order has been pursued :—I. The bony walls of the orbit. II. The anterior fibrous wall,—namely, the septum orbitale and the tarsal plates. III. The skin, the surface anatomy, including the movements of the lids, asymmetry, the vascular and nervous supply of the skin. IV. The orbicularis, the conjunctiva, and the intermediate structures of the lids, including the expansion of the levator palpebræ. V. The lacrymal apparatus. VI. The course of the optic nerve. VII. The muscles. VIII. Tenon's capsule, the expansions from the sheaths of the muscles, the fasciæ and fat of the orbit. IX. The arteries, veins, and lymphatics. X. The nerves. XI. Synopsis of the topography of the contents of the orbit.

It has seemed wisest to pass lightly over the more elementary facts of anatomy, paying attention rather to those not generally stated, and to treat the matter to a great extent topographically.[1]

I.

The bony framework of the orbit is important as a whole. The practitioner needs to know which parts are strong and which are weak, also what is to be found on the other side of the walls. The orbits are roughly described as pyramids, the bases of which are at the openings, so placed that the inner walls are parallel and that their axes diverge as they go forward. This is in the main true, only it must be observed that though the base is quadrilateral the angles inside are rounded off, and that most transverse sections show the orbit to be more of a cone than of a pyramid. The outline of the base is formed above by the frontal, the prominent external angular process of which joins the ascending process of the malar. At the upper inner angle this border shows usually something of a prominence, caused by the frontal sinus. At about the junction of the middle and inner thirds is the supra-orbital notch, or foramen. The vertical outer border and the outer half of the base are made by the malar, which has a

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[1] I wish to acknowledge the valuable services of Dr. Benjamin Tenney, who has made many dissections and measurements for this work.

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sharp orbital edge throughout. This is continued by the ascending sharp edge of the superior maxillary, which at the inner side of the orbit forms the front border of the lacrymal canal. This sharp ridge ends just before meeting the internal angular process of the frontal.

The inner border of the orbit is by no means always so easy to define. The preceding description applies very well to the female skull depicted in Fig. 1, but the other skull (Fig. 2) is very different. The superior border followed downward at the inner side of the orbit is continuous with the ridge of the lacrymal bone, forming the posterior border of the groove. As will be seen presently, this has an important bearing on measurements of the base of the orbit.

The lower inner angle is more rounded than the others. The one above it is the sharpest. The upper and lower borders generally slant downward as they pass outward. Both the shape and size of the base of the orbit vary considerably. Broca introduced an orbital index which is the ratio of the height to the breadth of the base, thus: $\text{index} = \frac{\text{height} \times 100}{\text{breadth}}$. If the index is below 84 it is microseme, from 84 to 89 mesoseme, and above 89 megaseme. A large index means a high orbit. The index of English skulls is given as 88. Fig. 1 shows a Roman female skull in which the orbital index is remarkably high, 106. Fig. 2 is that of a Caucasian with a pretty low index, 73. These may serve to show two extreme forms, but the latter is much less noteworthy than the former. The height of the orbital opening is easily measured. Unfortunately, there is a vagueness and discrepancy in the directions for measuring the breadth. Flower gives the inner point as that where the crest bounding posteriorly the lacrymal groove strikes the suture below the frontal bone. This has the great fault of excluding the lacrymal canal from the orbit, in which it certainly belongs. Broca takes the dacryon,—*i.e.*, the point at which frontal, inferior maxillary, and lacrymal bones touch. This would include the groove, and yet he states that it is not in the orbit. The skulls represented were measured from the dacryon.[1]

The axes of the orbits are not parallel like those of the eyeballs. They diverge considerably. If prolonged backward they meet near the sella turcica at an angle of from forty-two to forty-four degrees. The axes, moreover, run downward as well as outward in their course from the apex to the base, forming an angle of from fifteen to twenty degrees with the horizon. It has been thought that greater divergence is found in shorter skulls, but this is not certain. The roof of the orbit is in the main more nearly horizontal from before backward than the floor. It is not a straight line, but a sinuous one curving upward in the middle. The cavity is more or less overhung by the superior border. The degree of overhang is very uncertain. There is next to none in the Roman skull, and a great deal in

[1] Topinard, Eléments d'Anthropologie générale, 1885.

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Fig. 1.

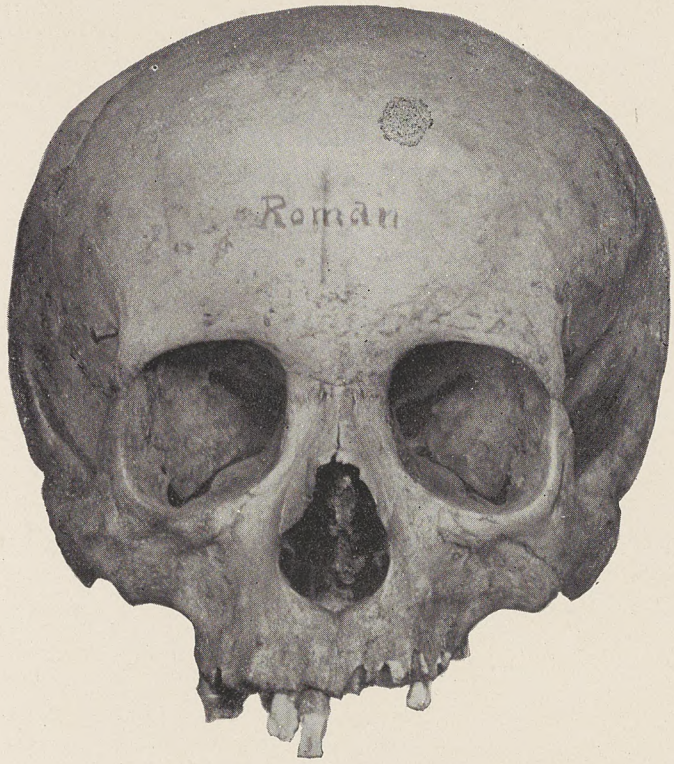


Fig. 2.



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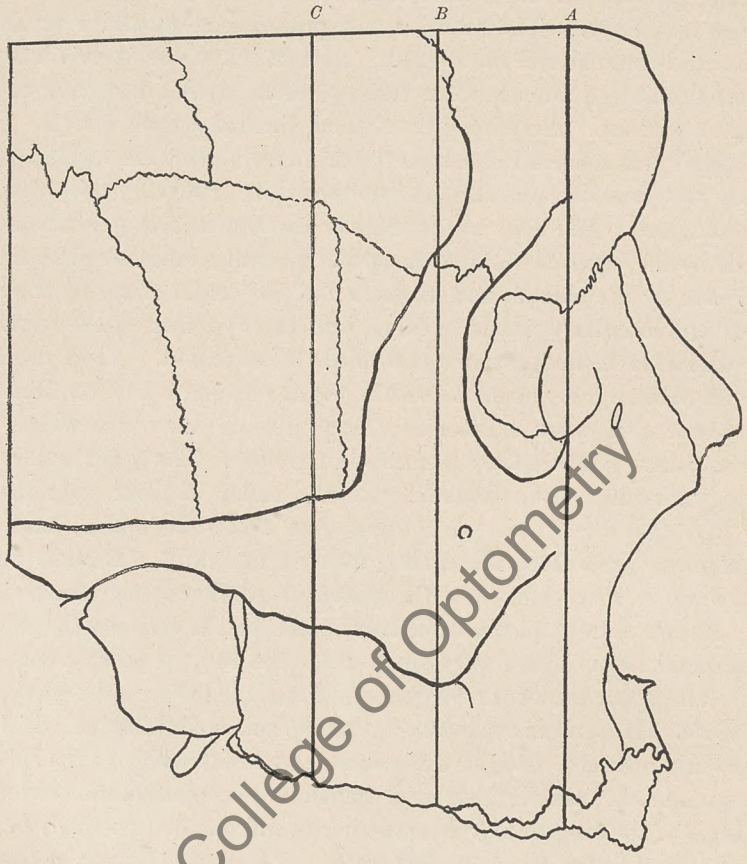
the other. It is deepest at the outer angle, but it is not unlikely that it is most marked in skulls with large frontal sinuses, like that of Fig. 2. When large, these may expand throughout the front half of the roof. This is otherwise thin as paper, though thickened by irregular ridges on its cerebral surface. The inner wall is vertical. It joins the roof above at almost a right angle, while below it passes by a gradual curve into the floor. It is made chiefly by the orbital plate of the ethmoid. A small part of the sphenoid is behind this. In front of it is the lacrymal bone, which consists of two parts. The hind one is in the same plane as the ethmoid. The front one, separated from the other by a ridge, forms a part of the lacrymal groove, which is completed by the ascending process of the superior maxillary. The anterior and posterior ethmoidal foramina are between the ethmoid and the frontal. Almost the whole of this wall is of extreme thinness, quite unable to resist pressure, as of a tumor, from either within or without. Anteriorly the frontal sinus descends into it. Below and behind this the wall separates the orbit from the nasal cavity. Occasionally the ethmoidal plate bulges into the orbit. Probably this, if marked, is pathological. The floor slopes more or less downward and outward. It is made by the superior maxilla, excepting a small triangular piece near the apex made by the palatal, and its outer anterior angle made by the malar. The spheno-maxillary fissure opening into the zygomatic fossa bounds the floor externally in the posterior two-thirds of its extent. From this fissure the infra-orbital groove runs to within one or one and a half centimetres of the anterior wall, when it becomes a canal passing under the orbit. Very often its course is marked by a suture in the floor. The outer wall is made by the great wing of the sphenoid with the malar in front. At the very back part, the edge of the great wing, just below the sphenoidal fissure, separates the orbit from the middle fossa of the skull. Beyond that the great wing is very thick, but the posterior portion of the malar is very thin. Rather more than the front half of this wall is between the orbit and the temporal fossa. Two very small foramina may be seen in the malar bone. The upper leads into the temporal fossa, the lower to the cheek. The apex of the orbit is near the lower end of the sphenoidal fissure, which runs upward and outward between the greater and lesser wings of the sphenoid. It opens into the middle fossa and transmits the ophthalmic vein and all the nerves of the orbit except the optic nerve and one or two small branches from the second division of the fifth pair. It is always largest at the inner end. It then narrows to a small slit, and usually, but not always, expands at the outer end. Sometimes the narrowing is slight and the enlargement wanting. The variations in shape depend chiefly on the lower edge. Just to the outside of the enlargement a more or less prominent spine serves for the attachment of a part of the external rectus (Fig. 1, left orbit). The optic foramen (Fig. 2, left orbit), the orifice of a short canal through the lesser wing of the sphenoid, opens just above and internal to the inner end of this fissure. Its diameter is about five millimetres

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transversely. It is often a little larger from above downward. The sphenomaxillary fissure is longer than the other, which it almost meets at the apex. It runs downward, outward, and forward, bounded by the sharp lower border of the great wing of the sphenoid above and the border of the maxillary below. It is closed in front by the malar bone. It often is enlarged at this point.

In view of the importance of the topographical relations of the bony walls of the orbit, three frontal sections through this region have been made for this work. The vertical lines *A*, *B*, and *C* on Fig. 3 show their

Fig. 3.



positions on the surface. Each of the three following figures shows the front of each slice at the three lines: thus, in Fig. 4, all before *A* is taken off.[1]

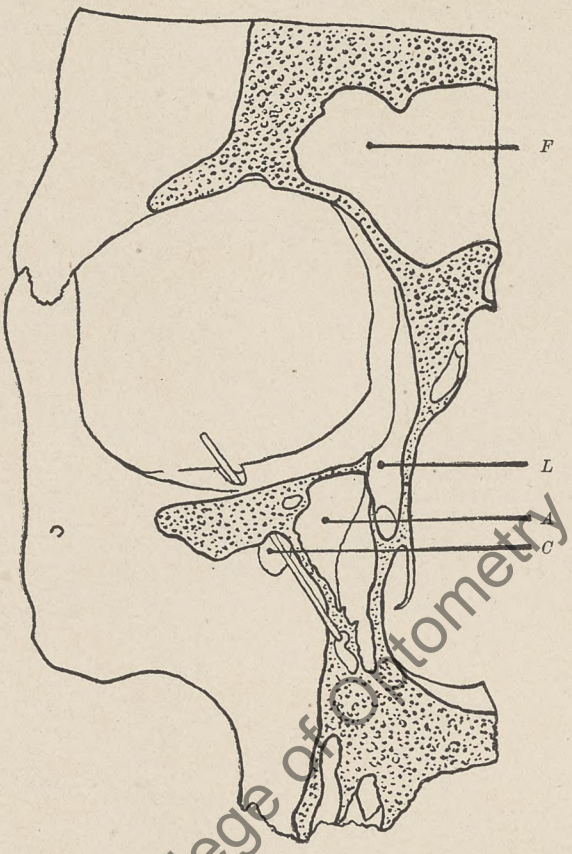
The first cut, Fig. 4, at *A*, strikes the bone at pretty nearly the middle of the orbital opening, a little outside of the supra-orbital notch. The outline of the orbit is even more quadrilateral than at the front, which

[1] Figs. 3, 4, 5, and 6 are a little larger than nature.

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is partly due to the section striking the lacrymal groove and canal, *L*, which appear at the inner side of the orbit. The canal opens into the inferior meatus just back of this plane. Above, at the inner side, is seen a well-developed frontal sinus, *F;* it reaches a little farther outward just back of this section. Below, we see a little of the antrum, *A;* external to this is the opening of the infra-orbital canal, *C*, four millimetres below

FIG. 4.



the floor, with a rod passed through it. Internal to this, under the floor, is a side branch, the anterior dental canal for the artery and nerve of the incisors.

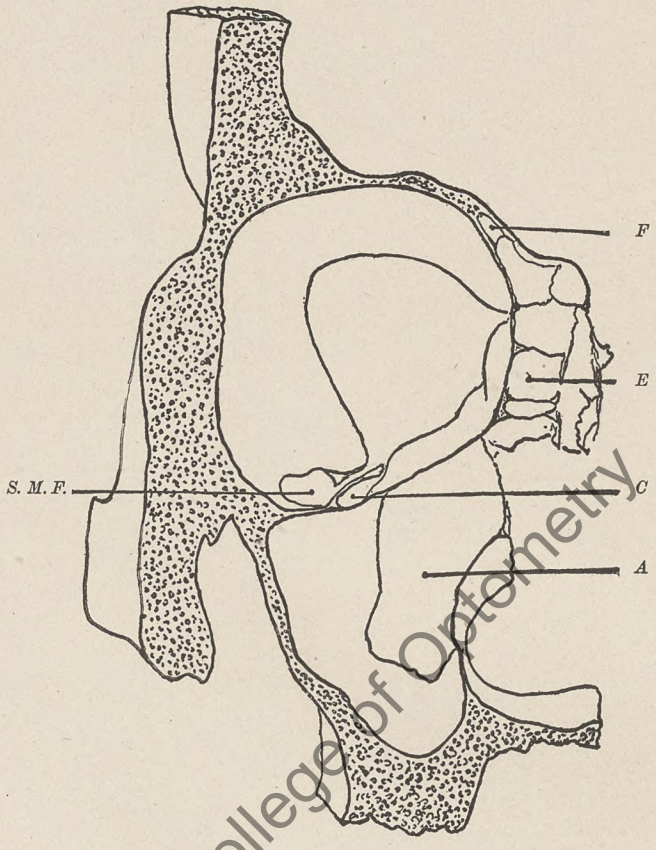
Fig. 5 shows the section at *B*. The inner angles are much rounded off. The obliquity of both roof and floor is striking. At the inside are the ethmoidal cells, *E*. Above and external to these, hardly visible, is the extreme posterior point of the frontal sinus, *F*. In the floor is the infra-orbital groove, *C*, which becomes a canal in the thickness of the slice just removed. The extreme delicacy of this floor separating the orbit from the antrum, *A*, needs no comment. The apparently great thickness of the outer

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wall is owing to the way in which the section has divided the orbital process of the malar. Behind this is seen the flaring outer wall, and in the lower outer angle the front of the spheno-maxillary fissure, *S. M. F.*

Fig. 6, at *C*, cuts the orbit near its apex. The thickness of the outer wall is here due to the saw having passed through the great wing of the sphenoid just where it forms the front of the middle fossa of the skull. In fact, it has opened this at one point, *M. F.* Had it struck even one millimetre farther back, this cavity would have been shown as a rent

Fig. 5.

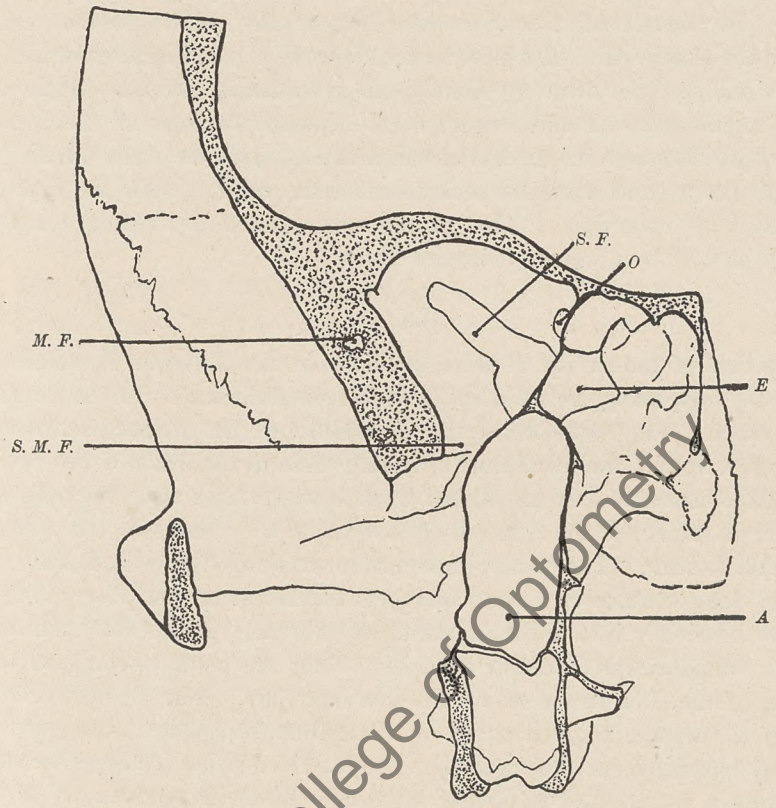


between the outer wall of the orbit and that of the skull. The spheno-maxillary fissure, *S. M. F.*, runs into the orbit below. Internal to this is the back of the antrum, *A*, with the last molar tooth just beneath it. The posterior ethmoidal cells, *E*, appear above the antrum at the inner wall of the orbit. The roof of the orbit is thicker here than in the preceding sections. At the apex of the orbit a part of the optic foramen, *O*, can be seen. External to this is the sphenoid fissure, *S. F.*, opening into the middle fossa of the skull between the greater and lesser wings of the sphenoid bone.

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The actual size of the orbit varies both with races and with individuals. It could hardly be otherwise, depending as it does on the shape and size of the face, one of the most variable parts of the body. Merkel puts the depth of the orbit at 43 millimetres in male skulls and 40.5 in female ones, but this applies only to those from certain parts of Germany. Other statements range from below 4 centimetres to 5 centimetres. The breadth at the base is given by Merkel at 40.5 millimetres for men and 40 for women, and the height at 35 millimetres for men and 34.5 for women. The height varies from 3 to 4 centimetres, and the breadth from 36 to 50

Fig. 6.



millimetres. It is to be remembered that the two orbits often differ in size and position. The female orbit, though absolutely rather smaller, is larger relatively to the face than the male one. Its outlines usually show the greater delicacy which is characteristic of the bones of the female face.

"If we contrast the front view of the face and cranium of the infant and the adult by counting as face all below a line at the tops of the orbital arches and as skull all that is seen above that line, considering it projected on a vertical plane as in a photograph, we find that in the infant the skull forms about one-half and in the adult much less. Coming to details, we

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find that the height of the orbit bears pretty nearly the same proportion to the skull at all ages, but that it equals barely a third of the adult face, while it makes nearly a half of it at birth. While the top of the nasal opening retains pretty nearly the same relation to the orbit at all ages, its lower border is but very little below the lowest point of the orbit at birth and much below it in the adult."[1]

Merkel, who has paid particular attention to the growth of the head in childhood, states that at five years the base of the orbit lacks only 2 or 3 millimetres of its adult height, which it gains usually in the next two years. The breadth, however, is not yet reached, so that the orbital index of the child is higher, or, in other words, the diameters are more nearly equal. The female orbit is more like that of the child. Moreover, in infancy the axis of the orbit is horizontal instead of slanting downward.

The walls of the orbit are lined with periosteum, which is firmly attached at the borders and loosely to the smooth surfaces of the bones. At the optic foramen the dura is continuous both with the outer sheath of the optic nerve and with the periosteum of the orbit. Both the fissures are closed by membrane. That of the spheno-maxillary fissure consists in great part of involuntary muscular fibres.

II.

The base of the cavity of the orbit, open in the skeleton, is closed in life by the lids, using the word in its widest possible sense. These consist of the tarsal plates (miscalled cartilages) which form the greater part of the lids proper, and of the membrane attaching them to the walls of the orbit. This whole structure may be likened to an optical diaphragm, the opening of which is the slit of the lids. It is covered on the outside by the orbicularis and the skin. The plates, lined on the inside by the conjunctiva, are made of dense connective tissue which gets thinner at the periphery, so that it passes insensibly into the surrounding membrane. Any strict definition of their boundaries is therefore artificial. They are about as long as the opening of the lids exclusive of the lacrymal bay. The breadth vertically of the upper is given as 10 or 12 millimetres, which is as good a conventional statement as is needed. The inferior, which is altogether less well defined, may be said to be half as broad. Both are convex, so as to fit over the eyeball. The membrane attaching these to the orbit is best called septum orbitale (*ligament large des paupières*). This, when dissected, appears as a strong unmistakable membrane in the upper lid. It is much more delicate in the lower. In microscopic sections it is hardly to be distinguished (Fig. 17, *Sep. O.*). It is treated diagrammatically in Figs. 18 to 21.

The septum orbitale is attached along the border of the orbit at the lower

[1] Archives of Pediatrics, September, 1891. The Neck and Head in Infancy, by Dwight and Rotch.

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and outer sides, and more or less within it at the inner side and above. It is generally incorrectly represented both as to its origin, which is put at the edge or even at the outer surface of the top of the orbit, and as to its direction. The upper part is not vertical in any position of the lid, but slants backward and then turns forward at an angle with its former course before it is lost in the tarsus. The external palpebral ligament (Fig. 16, *E. P. L.*) is a badly-marked thickening of some fibres of this membrane at the outer angle of the lids, running to the malar bone. The inner palpebral ligament (Fig. 16, *I. P. L.*) is a true and important band. It lies on the septum orbitale, with which it is inseparably connected. It runs from the inner ends of the tarsi to the superior maxilla in front of the nasal groove. When made tense by pulling the lids outward, it shows clearly through the skin which is attached to it. It is attached posteriorly through the septum orbitale to the anterior surface of the lacrymal sac. This ligament is the same thing as the direct tendon of the orbicularis. There is also a membranous expansion passing behind the lacrymal sac to the crest on the lacrymal bone, which is often called the reflected tendon of the orbicularis.

III.

The region of the eye as studied on the living is bounded above by the eyebrows, externally by the border of the orbit. It is separated from the cheek below by a curved line, hardly to be seen in the young and fat, but very clear in others. Internally it is bounded by the projecting nose. The eyebrows, generally nearly straight, except in the outer part which slants downward, but sometimes decidedly arched throughout, are of very varying development. They are composed of coarse stiff hairs pointing outward. The inner half corresponds pretty closely to the upper border of the orbit, but the outer half, on account of the downward slope of the orbit, is above it, resting against the forehead. Sometimes the outer half is wanting. Sometimes, especially in dark-haired races, the eyebrows meet at the root of the nose. The inner half is the strongest and thickest. At the outer end the hairs are fewer and smaller. The lower hairs slant upward, and the upper downward as well as outward. Thus they meet to make a raised crest in the middle. The shape depends largely on the direction of the outer end. The eyebrows are but little developed in infancy. They rarely are strong in childhood. At about puberty they become more marked. The hairs grow longer and coarser throughout life, especially in men. In women this feature is more delicate. Individual differences are endless.

Just above the eyebrows over the inner half of the orbit may be felt the superciliary eminences. The skin here is thick and but very loosely attached to the bone, so that it follows the pull of the muscles which are practically in it. Thus the eyebrows may be raised well on to the forehead by the frontalis, or brought far down over the orbits by the orbicularis. The skin at the outside of the orbit, as well as below it, is thinner, and is also loosely fastened so as to be easily thrown into folds. The slit of the

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eyelids may be closed by drawing the skin directly outward. At the side of the nose the thin skin is more adherent than elsewhere, but even here some displacement is possible. The skin, becoming thinner, turns in under the upper border of the orbit to form a deep furrow where it again turns forward over the tarsus. The amount of overhanging tissue varies much. It is one of the characteristic points of a face, generally increasing with age. Photographs from life show how this fold is deepened as the eye is turned up. When the eye is closed the fold is practically effaced, but after early youth one or more creases remain (Fig. 8). The lid of the infant (Fig. 22) contains much fat, which later generally disappears. With its absorption and the loss of elasticity of the tissues, folds and wrinkles increase. Towards the edge of the lids the skin is closely adherent to the tissues beneath it. The furrow already alluded to below the eye, though following the general curve of the lower border of the orbit, is not opposite to it, but distinctly (almost one centimetre) lower down. After middle age another smaller fold above it shows approximately the lower border of the tarsal plate. The peculiar dark discoloration which often is seen below the inner angle in varying degrees under different circumstances is not easy to account for. It has been ascribed to venous stasis. In some cases this explanation may be satisfactory, but not in all. It seems as if there were an actual change in the color of the skin. The opening of the lids is, roughly speaking, oval, the length being from twenty-five to thirty millimetres and the greatest breadth from twelve or less to fourteen millimetres. Both the actual size and the proportions of the opening vary considerably. Usually all but the upper part of the cornea is uncovered in most persons. The inner angle or canthus presents a little bay, due to a change in direction in each lid, in which lies a raised pinkish little body, the lacrymal caruncle. In infancy the lacrymal bay is rudimentary and the vertical height of the opening large relatively to the length, which gives the well-known appearance of large eyes of babies. The lids of the open eye meet at the same level. That is to say that, the eye being open, the upper lid does not overlap the lower at the outer angle, though a little fold and the line of the eyelashes seem to suggest it. The lashes of both lids stop a little short of the lacrymal bay. Those of the upper lid, much the larger and more numerous, spring in several rows from the under edge of the lid and turn upward. Those of the lower lid arise from its anterior surface near the edge and are directed forward and downward. There is a peculiarity of the lower lashes that is significant when the closing of the lids is considered. It is that the line of insertion of these lashes is farther from the edge of the lid at the outer part than at the inner. Both lids have the longest lashes in the middle. The curve of the edge of the upper lid is much greater than that of the lower. Not only is the outer canthus generally the higher, but the axis of the lacrymal part often slants a little downward and inward. When the eye is closed certain remarkable changes in these relations occur. The upper lid falls a great

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Fig. 7.

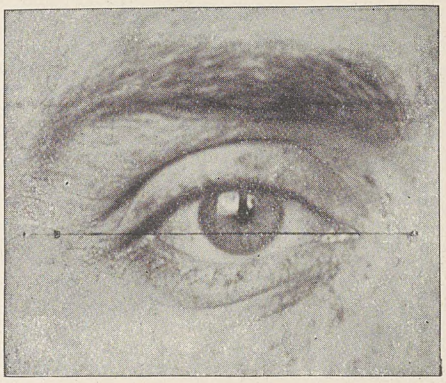


Fig. 8.

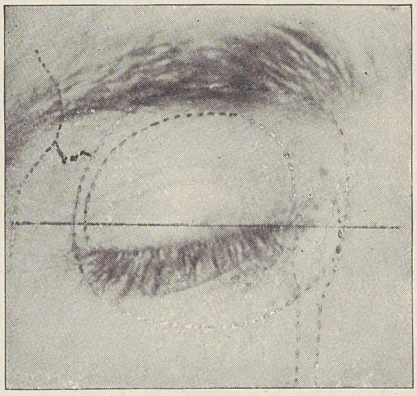


Fig. 9.

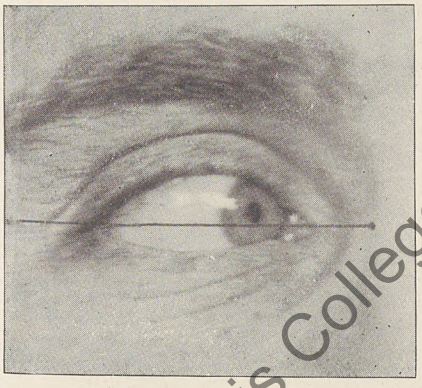
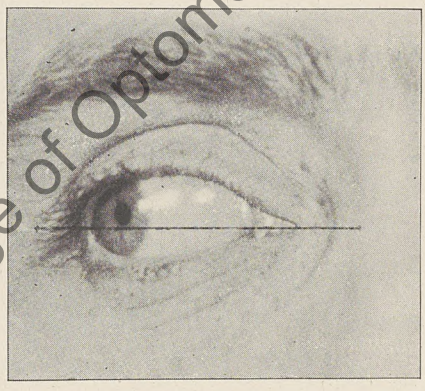


Fig. 10.

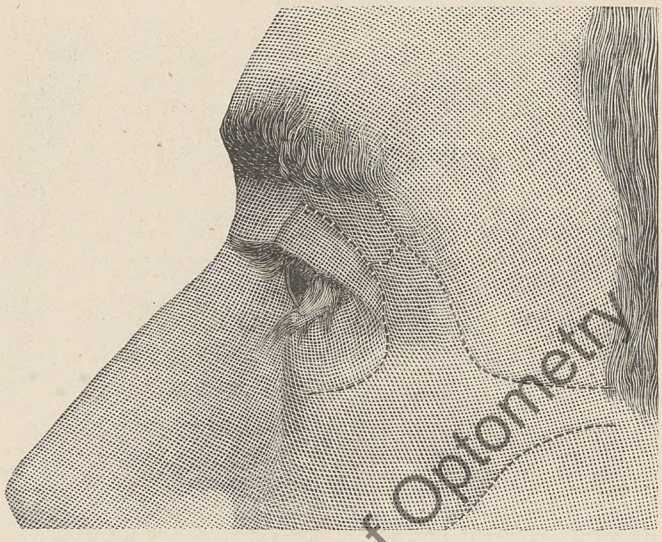


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deal; the lower lid rises a little. At the same time the lower lid is drawn somewhat inward, and thus at its outer end is for a short distance overlapped by the upper. The line of the joined lids describes a slight curve, rising and becoming straight at the inner end. The outer end of the slit has become distinctly lower than the inner. (See Figs. 7 and 8.) In watching the movements, one is struck by the fact that the inner canthus is practically still. A series of frozen sections through the closed lids (Figs. 18 to 21) shows—besides other things—that at the outer canthus the upper lid overhangs the lower when closed. It continues to do so, though in a constantly decreasing degree, as we pass inward. Thus the slit between the lids, from an angle of forty-five degrees, becomes nearly horizontal before the inner canthus is reached. It is to be noted that the edges of the lids are applied closely one to another throughout. There is no

FIG. 11.



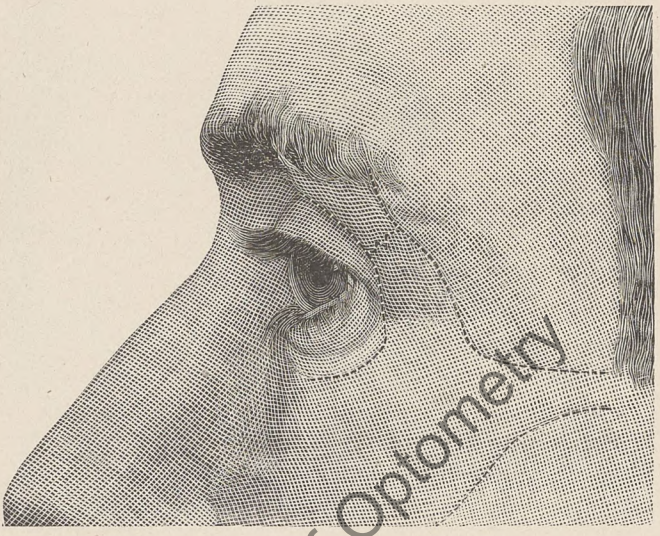
reason to believe in the three-sided canal which they have been supposed to form with the cornea for the passage of the tears. The changes in the position and shape of the lids in the other movements of the eyes deserve more attention than is generally paid to them. Every one knows how the rise and fall of the upper lid are associated with the corresponding movements of the globe, but it is not generally stated that the lids take part in the lateral movements. It is, however, certain that they do so. When the eye is turned towards the nose (Fig. 9) the inner canthus is drawn backward and inward; when the eye is turned out (Fig. 10) the outer canthus is pulled outward. The latter movement is the greater. The change in relation to the outer border of the orbit is shown conclusively in the profile views Figs. 11[1] and 12. This is the necessary result of the insertion into

[1] Figs. 11, 12, and 13 are from actual photographs.

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the lids and conjunctiva of the expansions from the sheaths of the outer and inner recti. The front views show also certain changes in the shape of the opening. When the eye is turned strongly outward (Fig. 10) the distance between the lids is greater than when it is turned strongly inward, except at the lacrymal bay, where the reverse occurs. When the pupil is turned out this is stretched and narrowed; when turned in (Fig. 9) it is expanded. The profile view of the eye looking up (Fig. 13) is a very instructive one in several respects. Apart from displaying the folding in of the upper lid, it shows that the lower lid rises also and becomes more prominent. The latter fact is due partly to its being in closer relation to the globe in this position and partly, perhaps, to its being crowded forward by a mass of solid fat in the lower part of the base of the orbit. These photographs suggest very strongly that in this forced looking upward the eyeball

FIG. 12.



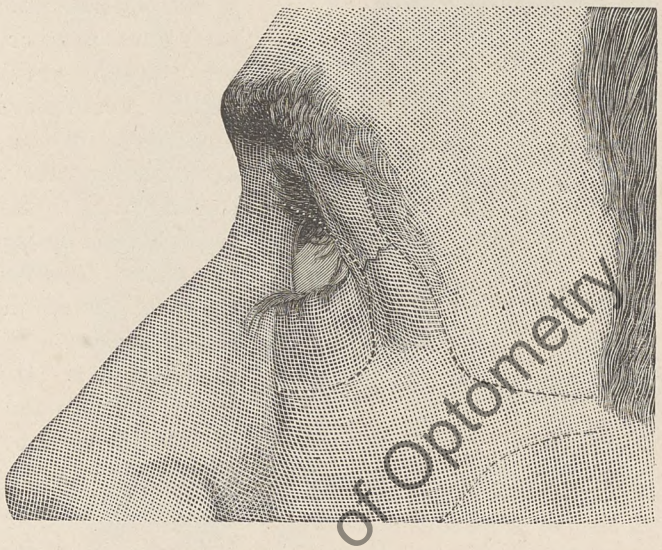
not merely rotates on a transverse axis, but is carried to a slight extent bodily upward. This effect is presumably an illusion.[1] The lids, both when open and when shut, are applied very closely to the globe of the eye, except at the lacrymal bay, where they leave it. The hardness and to some degree the shape of the eye are to be felt through the closed lids. The prominence of the cornea can in some cases be detected even by sight. The inner edge of the entire border of the orbit can easily be explored by the finger. Its relation to the surface is indicated in Fig. 8. The supra-orbital notch, when present, is more easily felt by carrying the finger outward, as its outer border rises the more suddenly. If there is a foramen

[1] This statement is made out of deference to the views of ophthalmologists. I can see no anatomical reason why in forced raising of the lid there should not be also a slight upward movement of the entire globe.

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it can be made out only by the sensations of the patient from pressure on the nerve, or possibly by the pulsation of the artery. The foramen may be as much as five millimetres above the edge. It is worth noting that in such cases the canal leading to the foramen does not necessarily begin far back in the orbit, but, on the contrary, may begin just within its margin. The upper edge of the zygoma and the posterior border of the malar bone are felt rather less distinctly. The external angular process of the frontal, however, is very plain, and usually the suture between it and the malar can be made out. It is recognized by a change of level, the angular process being a little more prominent than the top of the malar. Inside the upper inner angle the trochlea can be felt with some difficulty. Two very important practical points call for notice: first, the large size of the globe in proportion to the size of the orbit, and next its prominence. A vertical

Fig. 13.

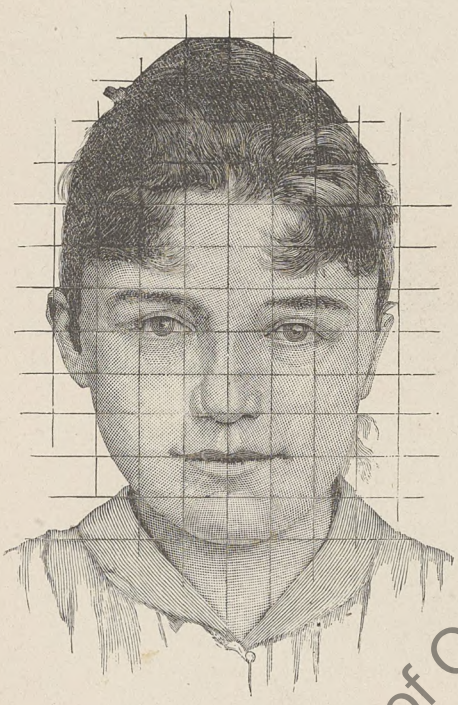


plane from the upper to the lower border of the front of the orbit would in some cases touch the front of the cornea, and in very prominent eyes pass through it. At the outside, owing to the divergence of the outer wall of the orbit, the globe is much uncovered. A vertical transverse plane at the outer edge of the orbit would pass near its equator. Fig. 29 is just in front of this. The projection of the upper angle of the orbit gives it a certain amount of protection, but still this side is comparatively unguarded. Various attempts have been made to recognize on the living the position of the optic foramina. One of the latest suggestions is that they are very nearly in a vertical plane passing through the two points at the greatest outward convexity of the zygomata. This will do for a rough method. If we evert the lids we see the little lacrymal papillæ with the minute orifices of the tear-ducts at the beginning of the lacrymal bay. They are directed

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somewhat backward, that they may be the better applied to the surface of the conjunctiva so as to suck up the tears. They are not precisely in the same vertical plane, but the upper is a little the internal, which admits of the more accurate closing of the lids. The little ducts run close to the edge of the lid on their way to the sac. This sac is so placed that its highest part extends somewhat above the internal palpebral ligament. The line of the axis and of its continuation, the nasal duct, must be studied both from the front and from the side. In a front view (Fig. 8) it crosses at the middle of the internal palpebral ligament and runs to near the end of a line extending into the furrow between the cheek and the ala of the nose at its widest point. According to the breadth of the nose, this line may be vertical, or incline somewhat outward, or even a little inward. It always slants more or less backward, and in a varying degree. Merkel would have the line representing it on a side view extend from the preceding starting-point to the space between the last bicuspid and the first molar. Luschka drew it to the space between the first and second molars. I incline to the latter view. It is needless to say that only the first part of this line corresponds to the duct.

Fig. 14.



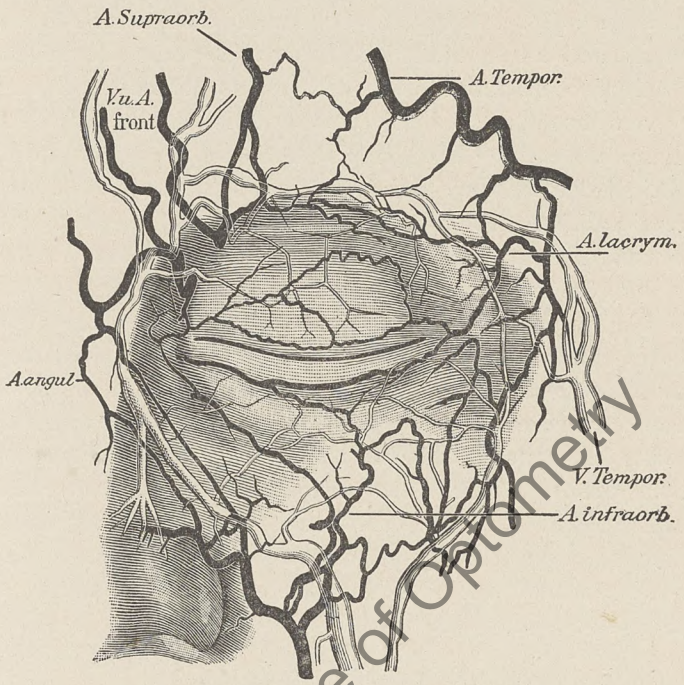
Before leaving the surface anatomy, the vexed question of asymmetry of the eyes must be touched lightly. This is to be seen almost always in the living if the face be looked at through a screen of wires at right angles. The right eye is probably usually the higher. According to Hasse, the left eye is nearer the middle line, whether it be the higher or the lower. One eye is often more open than the other. A want of symmetry is often found in the skull, but, for obvious reasons, it is less than in the flesh. The left orbit shows no approximation to the middle. One important factor in this question is generally overlooked,—namely, that there is not only a difference in height between the eyes, but that one orbit and cheek are anterior to the others. This complicates the problem strangely, making it often almost impossible to decide which position of the head is to be called normal. A striking instance is the above extremely uneven head and face (Fig. 14), of

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which, nevertheless, the asymmetry would easily pass unnoticed. To determine how much habitual position of the trunk or habitual use of one eye may account for this is by no means so simple as at first appears.

The arteries (Fig. 15) of the lids and adjacent parts of the face come from many sources, making a series of anastomoses beyond the margins of the orbit. The continuations of the ophthalmic and facial arteries at the inner side of the nose and a branch of the temporal near the outer upper angle are usually the largest. Branches running upward into the lower lid come from the facial, reinforced by anastomoses with the infra-orbital artery. At the outer angle are branches from the transverse facial and,

FIG. 15.



Arteries dark, veins light. (After Merkel.)

perhaps, from the orbital branch of the middle temporal. The ophthalmic artery of the internal carotid sends blood through the lacrymal branch to the outer part of the lids, through the frontal and nasal to the inner upper angle of the base of the orbit, and through the little supra-orbital to the upper part of this region. A delicate arch is found in each lid between the tarsus and the orbicularis. That of the upper lid is nearer the edge than that of the lower. These arches are formed by the meeting of the palpebral arteries from the inner side with branches of the lacrymal from the outer. A less regular arch in the upper lid may be found near the top of the tarsus. This system of vessels supplies all the structures of the lid and communicates in the conjunctiva lining it with the conjunctival vessels

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proper. Small arterial twigs are to be found both over and beneath the orbicularis.

The large frontal vein at the inner side of the orbit communicates with branches of the ophthalmic vein. (See, also, Fig. 32.) A branch connecting it with the anterior temporal forms an arch along the top of the orbit. The facial vein receives some distance below the orbit a vein from its outer border. The branches in the lids do not form definite arches like the arteries, but run in the main at right angles to the palpebral opening. It is, however, worthy of notice that the vessel marked *V* in Fig. 17, though of about the size and position of the one which Merkel describes as an artery forming the tarsal arch, is undoubtedly a vein. The artery lies a little higher. Merkel points out that most of the superior branches and all the internal ones pass through the orbicularis, so that its continued contraction must cause a congestion. Probably under these circumstances more of the blood passes off into the cranium or into the system of the internal maxillary vein, but under ordinary circumstances the current is superficial.

The lymphatics of the lids form two nets before and behind the tarsal plates. Of the few vessels crossing the face, some empty into the system of the parotid glands, and probably some into that of the submaxillary.

The sensory nerves of the upper lid and neighborhood come from the first division of the fifth pair. Above the orbit are the supra-orbital nerve, passing through the notch, and the supra-trochlear at the inner angle. Both of these send branches downward to the upper lid, which may also receive twigs externally from the lacrymal nerve. The infra-trochlear branch of the nasal nerve reaches the surface at the inner side of the upper lid above the palpebral ligament, to which it may or may not give branches, going chiefly to the side of the nose. The lower lid is supplied by several branches of the infra-orbital. The palpebral branches in both lids run in the main towards the slit, near which, according to Mises, they make a series of communicating arches. The motor branches from the facial reach the orbicularis from the outer side.

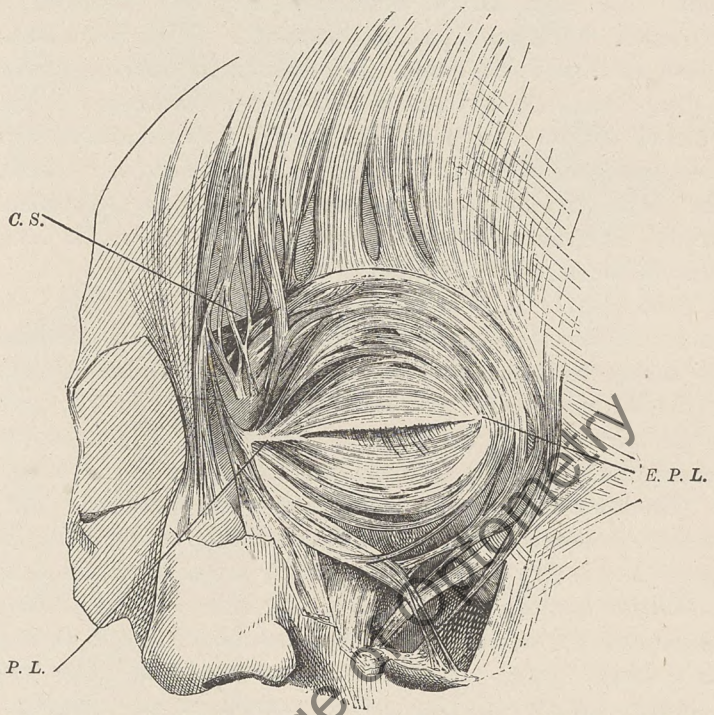
IV.

Beneath the skin lies the orbicularis palpebrarum, the superficial part of which may be divided into the palpebral and the orbital portion. The former is confined to the lids proper; the latter spreads out beyond the margin of the orbit, mingling with the muscles of the forehead and of the cheek. The palpebral portion arises from the internal palpebral ligament and from the front of the lacrymal sac as a series of delicate bundles of pale fibres somewhat scattered, so as not to form a continuous layer, which spread themselves in arches over the front of the tarsal plates, the inner ones ending in the fibrous tissue at the outer canthus called the external palpebral ligament, the outer ones describing complete loops. Fibres from the beginning of the band run upward to the forehead and downward to the skin of the cheek. Some few bands of fibres running in a group by

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themselves near the margin of the lid have been called the ciliary muscle of Riolan. It is well shown in the sections of the lid, Figs. 17 and 22, *R*. What is usually described as Horner's muscle (5 in Fig. 23) is best considered as a deep head of the orbicularis which arises from the crest of the lacrymal bone behind the sac, over which it spreads, to send some fibres to the inner ends of the tarsi, while others mix with those of the superficial set. Some fibres twine themselves around the tear-ducts. Horner's muscle should be dissected from behind. The portion going to the upper lid is much the larger, and placed back of the lower.[1] The palpebral portion of the orbicularis closes the lids gently, as in unperceived winking. The deep

FIG. 16.



Orbicularis palpebrarum.—The palpebral and orbital portions are easily recognized, though the line of separation is not always to be seen. *C. S.* points to the corrugator supercilii; *I. P. L.*, internal palpebral ligament; *E. P. L.*, position of external palpebral ligament. (After Henle.)

portion draws the lids inward, which is sometimes evident in the early part of the process of closing them. A few people have the power of contracting it independently, so as to draw the lids inward and narrow the slit without closing the eye. The tonicity of the whole palpebral portion affords a support to the globe. The orbital portion is continuous with the former. Some of its inner fibres arise from the inner ligament, others from the inner border of the orbit above and below it. It overlaps the borders

[1] Fig. 23 is useful, but very diagrammatic. The two parts of Horner's muscle are not in one plane, as there represented.

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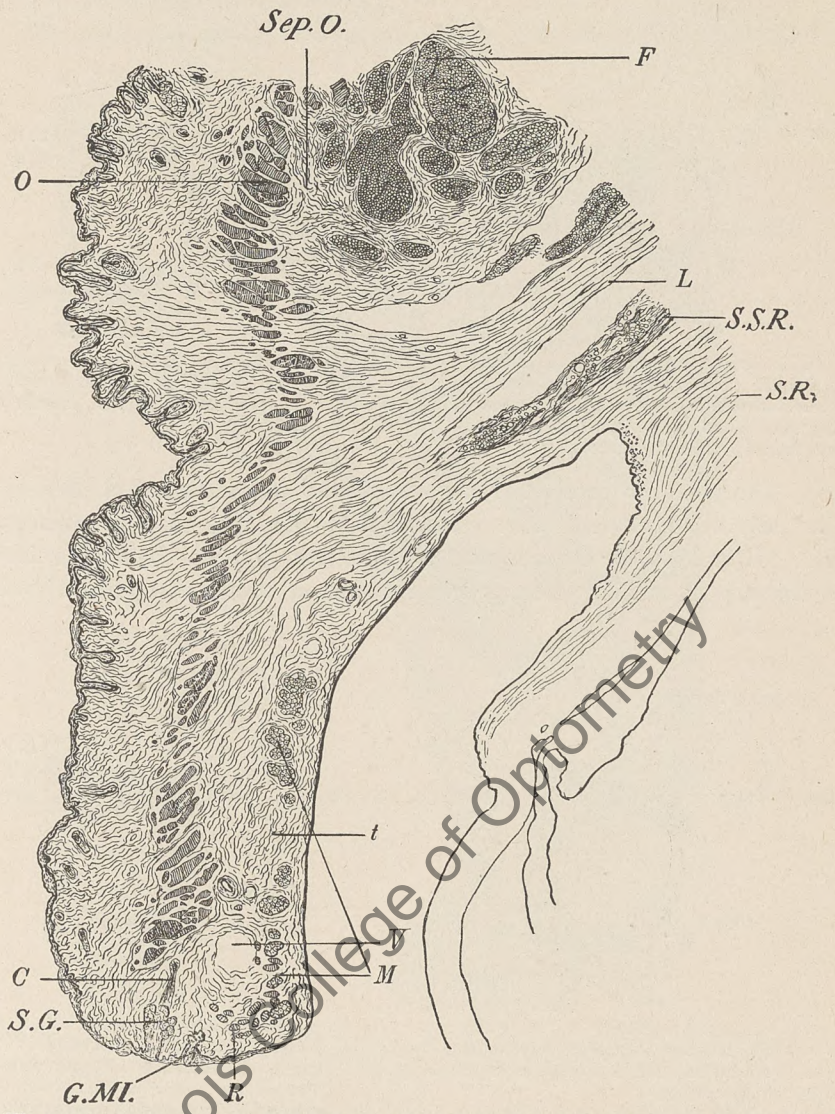
considerably, except at the inner side. Some of its fibres make loops surrounding the orbit, open only at the inner end; others mingle with the neighboring muscles, as shown in Fig. 16. The corrugator supercilii (*C. S.*, Fig. 16) arises from the superciliary ridge just outside of the glabella. Its fibres run outward through those of the frontalis and orbicularis, which cover it, into the skin over the middle of the orbit, to draw it by its contraction into vertical folds. These muscles are supplied by the facial nerve.

The lids must now be considered comprehensively. They contain the following layers: first, the skin; second, the orbicularis; third, the tarsus and septum orbitale; fourth, the conjunctiva near the opening, and farther from it Müller's muscle, and in the upper lid the expansions of the levator palpebræ. The skin and the orbicularis have been described; the palpebral portion of the latter rests on the tarsus. There is but little areolar tissue between them in the adult. It is different, however, beyond the tarsi. There is much loose areolar tissue on both sides of the septum orbitale, which is the seat of effusion in œdema. The layer of the tarsi and the septum has also been described, with the exception of certain features at the border of the lids. It is important to observe that in microscopic sections the septum disappears. It seems to have no recognizable limits. At the border most anteriorly is the layer of the roots of the eyelashes (Fig. 17, *C*). These, two or three deep, lie in front of the lowest part of the tarsus. Sebaceous follicles (*S. G.*) and the so-called glands of Moll (*G. Ml.*)—modified sweat-glands—are among them. In a deeper layer, actually embedded in the tarsus (*t*), are the Meibomian (*M*) glands (see also Figs. 22 and 23), opening in a row in the deeper part of the border of the eyelid. These two rows are so distinct that the lid can be split by an incision between them without hurting either. The lower lid shows the same features less developed. The delicate conjunctiva becomes continuous with the skin at the border of the lids. The attachment here is very close, but it gradually becomes less, till near the line of its reflection towards the globe it is very loose. There is here more or less subconjunctival areolar tissue. The course of the line of reflection along the lids is worth noting. It extends one or two millimetres beyond the outer canthus, but does not pass the inner canthus at all. Beginning at its outer end, just beyond the canthus, it rises and falls rapidly behind the upper and lower lids respectively. Its reflection may be traced on the series of sections shown in Figs. 18, 19, 20, and 21. In Fig. 18, some 2 millimetres inside the outer canthus, it is 14 millimetres above the outer line of closure of the eyelids and sinks 2 millimetres below it. At about the middle of the opening (Fig. 20) it is 17 millimetres above and 4 millimetres below. At the beginning of the lacrymal bay (Fig. 21) it is 9 millimetres above and about 3 millimetres below. (These measurements show the line of reflection projected on a vertical plane measured from the edge of the upper lid, which, as these sections prove, overlaps the lower.) If we measure the breadth of the inner surface of the lids to the reflection of the conjunctiva, we find the greatest distance in the upper

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lid 18 millimetres and in the lower 8.5 millimetres. The line of its reflection is dotted on Fig. 8. The explanation of the short distance which it reaches below the eye is in the foreshortening resulting from the forward projection of the lower lid. It is not impossible, however, to hold

FIG. 17.



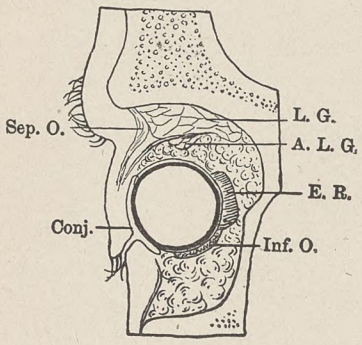
Microscopic section of the upper lid and front of the eye, by Dr. H. P. Quincy. *C*, eyelash; *F*, fat; *G. Ml.*, gland of Moll; *L*, levator palpebræ; *M*, Meibomian glands; *O*, orbicularis; *R*, ciliary muscle of Riolan; *Sep. O.*, septum orbitale; *S.G.*, sebaceous gland; *S.R.*, superior rectus; *S.S.R.*, sheath of superior rectus; *V*, vein.

that this line might have been drawn a trifle lower. The conjunctiva, after its reflection, comes soon into contact with Tenon's capsule. At the distance of some three millimetres from the cornea they are inseparably

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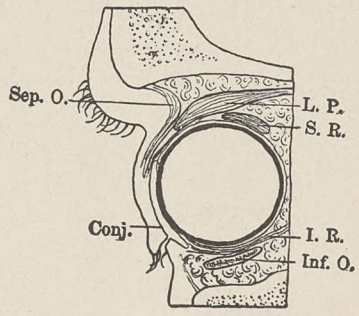
connected into a single membrane closely attached to the front of the eye. At the inner canthus, external to the lacrymal bay, there is a vertical curved fold of conjunctiva, called from its shape the plica semilunaris, which is drawn forward when the eye is turned outward (Fig.

FIG. 18.



L. G., lacrymal gland; *A. L. G.*, accessory gland. The expansion of the levator is seen between these. *E. R.*, external rectus; *Inf. O.*, inferior oblique; *Conj.*, conjunctiva; *Sep. O.*, septum orbitale.

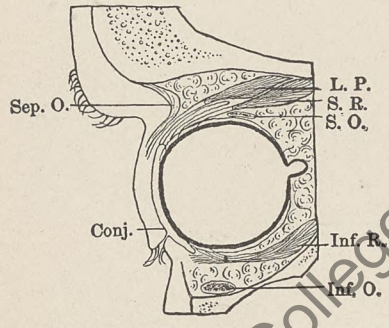
FIG. 19.



L. P., levator; *S. R.*, superior rectus; *Sep. O.*, septum orbitale; *Conj.*, conjunctiva; *I. R.*, inferior rectus; *Inf. O.*, inferior oblique.

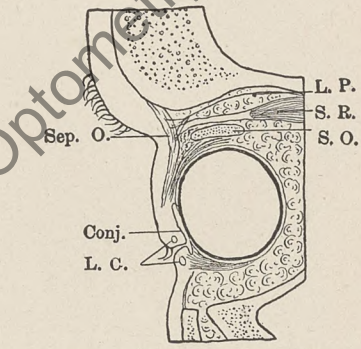
10). There are no arteries of any size in the conjunctiva, but there is a very rich net-work of minute vessels which come into view in inflammation. It is noted for its irregular arrangement, and may be distinguished by this and its mobility from a deeper system of vessels connected with the

FIG. 20.



Sep. O., septum orbitale; *L. P.*, levator; *S. R.*, superior rectus; *S. O.*, superior oblique; *Conj.*, conjunctiva; *Inf. R.*, inferior rectus; *Inf. O.*, inferior oblique.

FIG. 21.



Sep. O., septum orbitale; *L. P.*, expansion from levator; *S. R.*, superior rectus; *S. O.*, tendon of superior oblique. The oblique course of this tendon accounts for its apparently excessive thickness. *Conj.*, conjunctiva; *L. C.*, lacrymal canals.

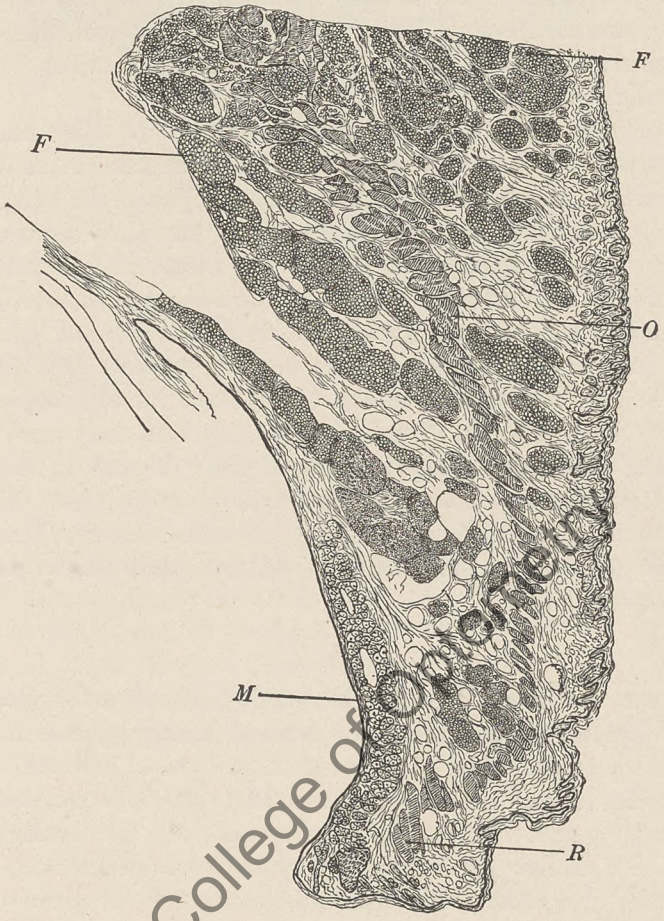
interior of the eyeball. There is a considerable plexus of lymphatics which is in communication with lymph-spaces of the cornea. The nerves of the conjunctiva are from the lacrymal and from the supra- and infra-trochlear branches of the nasal.

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(Figs. 18 to 21 are inserted here because, among other things, they show the levator and the superior rectus. They show many points of the topography of the orbit. They are in series from without inward, 18 being just inside the outer canthus and 21 at the beginning of the lacrymal bay. They are made from actual frozen sections. The treatment is necessarily diagrammatic.)

We come now to Müller's muscle, and to the expansions into the lids

Fig. 22.



Microscopic section through the upper lid of a negro infant, by Dr. H. P. Quincy. *F*, fat; *M*, Meibomian gland; *O*, orbicularis; *R*, ciliary muscle of Riolan.

from the levator palpebræ and from the superior and inferior recti. First as to the upper lid. The sheath of the superior rectus is at first closely connected with the under surface of the levator (Figs. 20 and 21). The superior rectus, *S. R.*, besides its insertion into the globe, sends fibres to the top of the fold of the conjunctiva, which is thus pulled upward and backward in harmony with the turning up of the eye, and from its sheath, *S. S. R.* (Fig. 17), fibres pass to the top of the tarsus. The levator, *L*,

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broadens out into an expansion stretching across the whole orbit from one bony wall to the other, which by its outer portion separates the greater lacrymal gland from the accessory portion below it (Fig. 18). This expansion splits into two layers. The greater portion, consisting of involuntary muscular fibres (Müller's muscle), is inserted into the upper portion of the tarsus, while certain anterior fibres pass into or through the fibres of the orbicularis to the skin of the lid. Their function is to draw the skin to the fold above the tarsus when the lids are opened. The expansion of the levator passing to the tarsus consists largely of unstriped muscular fibres mingled with elastic tissue. This is connected with other involuntary fibres arranged transversely, the whole constituting what is known as Müller's muscle.

The inferior tarsus is smaller than the upper, the Meibomian glands less developed. There is a collection of involuntary fibres known also as Müller's muscle which is of little importance. Fibres from the sheath of the inferior rectus may be traced, in sections of the lid, to the tarsus. According to Schwalbe, the termination of the sheath of the inferior rectus may be divided into three layers somewhat analogous to those of the upper lid, the middle one containing unstriped muscular fibres and going to the tarsus. The lid of the infant differs in some respects from that of the adult. Fig. 22 represents a section through the lid of a negro child at birth. As Figs. 17 and 22 are equally magnified, they show that the thickness of the lid at the edge is nearly as great at birth as in the adult. The most striking differences are the relatively small size of the infant's muscle and the great collections of fat in the areolar tissue. This accounts in a great measure for the thickness. In the infant also the Meibomian glands are very large.

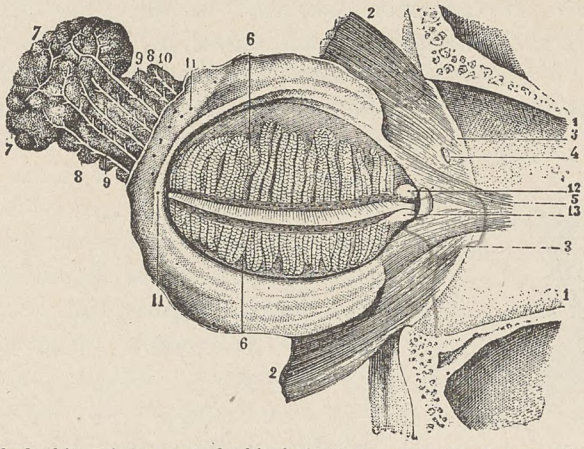
V.

The tears are secreted by the lacrymal gland, which, enveloped in its sheath, is situated under cover of the external angular process in a shallow pit in the top of the orbit. It consists of two parts, of which the larger is placed above and external to the smaller, which is sometimes called the accessory gland. A part of the expansion of the levator palpebræ separates the smaller gland from the larger, without, however, quite dividing them (Fig. 18). The greatest diameter of the gland is, on the average, 2 centimetres. It is situated above the conjunctiva and outside of the expansion of Tenon's capsule. The ducts of the larger gland pass through the smaller and receive communications from it. The chief ducts are some three or five in number, but with them are a few smaller ones (Sappey). These pierce the conjunctiva under the outer part of the upper lids. The lacrymal canals (Figs. 21, 24, and 25) which collect the tears begin at the points of the minute lacrymal papillæ, which are almost opposite to each other at the beginning of the lacrymal bay. The papillæ are directed obliquely inward towards the globe. The opening in the upper is

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somewhat the smaller. The first part of the duct is vertical, running upward in the upper lid and downward in the lower for some 2 millimetres. They then, turning at a slightly acute angle, run horizontally for 5 or

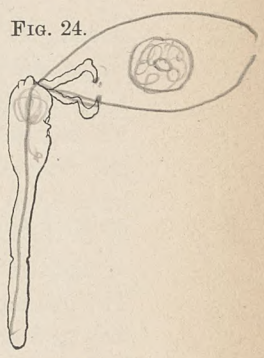
FIG. 23.



1, Inner wall of orbit; 2, inner part of orbicularis; 3, its origin from inner wall; 4, small opening for nasal artery and infra-trochlear nerve; 5, Horner's muscle (note remarks in text); 6, Meibomian glands; 7, lacrymal gland; 8, its accessory portion; 9, chief ducts; 10, ducts of accessory portion; 11, openings of the ducts; 12 and 13, lacrymal papillæ. (From Sappey.)

6 millimetres to the sac, which they may enter either separately or, as is probably the more usual occurrence, by a common termination (Fig. 24). There is a dilatation at the junction of the vertical and horizontal portions which is called a diverticulum. The horizontal part hardly deserves this name, for the ducts converge to their point of junction. It is evident that if the eye is closed they are more nearly horizontal and parallel than if it is open. Horizontal sections (Fig. 25) show that the superior canal is curved, with the convexity in front, while the lower is about straight. They enter the tear-sac just behind the outer end of the internal palpebral ligament. On their way they run close under the thin skin at the edge of the lids, surrounded by spiral muscular fibres from Horner's muscle, by which they are compressed many times a minute in unconscious winking (Krehbiel). As to size, the superior point is .2 millimetre in diameter, the inferior, .25. Less than a millimetre farther on, both are narrowed to .1 millimetre. The diameter then increases to .6 millimetre. The widest portion is the collecting tube, the width of which is in inverse ratio to its length. The lacrymal sac is situated in the groove at the inner side of the orbit (Fig. 25). Its continuation in the canal is called the nasal duct. There is a pretty well marked contraction at the end of the sac, the duct being smaller. A vari-

FIG. 24.

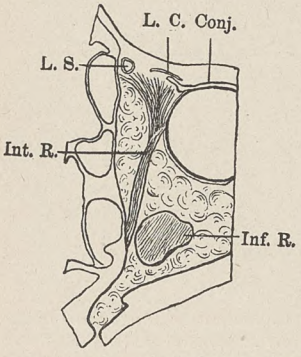


Tear-sac from a metal cast in the Warren Museum of the Harvard Medical School.

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able fold is sometimes found between the two. The sac extends upward some 2 or 3 millimetres above the internal palpebral ligament. The direction of the canal and the position of the sac have already been described in the surface anatomy. On the back of the sac lies the belly of Horner's muscle, arising from the so-called reflected tendon of the orbicularis. It is very doubtful if its contraction compresses the sac. The diameter of the sac when distended is some 6 or 7 millimetres, its length about 12 millimetres. The length of the succeeding nasal duct is very variable. According to Von Gerlach, it is from 12 to 14 millimetres,—about the same as that of the sac. He states that it is often prolonged at the lower end in the thickness of the mucous membrane, so as to reach a length of 20 millimetres. The nasal duct in the cast which we figure is even longer, 23 millimetres. Its greatest diameter is 4 millimetres. Frozen sections (Fig. 25) show clearly that in the undistended state the antero-posterior diameter of both sac and duct exceeds the transverse. A system of veins surrounds the duct in its canal. Henle cited it as an instance of what he called compressible cavernous tissue. It gives a support to the walls, and probably when congested can quite compress the cavity. The opening of the duct under cover of the inferior turbinate bone varies in shape and position. Perhaps it is most frequently a vertical or an oblique slit. Sometimes it is a transverse line under a fold of mucous membrane which is practically a valve. It does not always end with the bony canal, but may run for a variable distance in the mucous membrane. The distance from the posterior border of the nasal opening is given by Arlt as 30 or 35 millimetres, by Von Gerlach as 28 or 30 millimetres. In no one of eight measurements by Dr. Tenney was it as much as 28 millimetres.[1] The distance from the front of the inferior turbinate is given by Von Gerlach as 8 or 10 millimetres. Our measurements of ten specimens gave an average of a little less than 12 millimetres. The extremes were 10 and 16 millimetres. Valves have been described in various parts of the tear-passages. They are for the most part irregular and inconstant folds. The most constant and the best marked seems to be at the junction of the sac and the nasal duct. It is rarely, however, a perfect valve. The opening at the duct into the inferior meatus, while presenting no true valve, is of a nature to impede regurgitation.

Fig. 25.



Horizontal section through inner half of right orbit.—*L. S.*, lacrymal sac; *L. C.*, lacrymal canal; *Conj.*, conjunctiva; *Int. R.*, internal rectus and expansion from its sheath; *Inf. R.*, inferior rectus.

[1] Perhaps the reason for this discrepancy is that these measurements were made from the junction of skin and mucous membrane.

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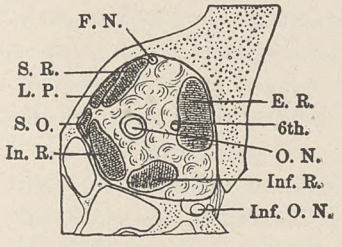
VI.

The optic nerve passes from the optic foramen in a slightly sinuous course downward and outward to the globe. As it descends it passes somewhat beyond what would be a straight course, so that it has to bend in again. There is much variation in the amount of these curves, which, in fact, may differ in the two eyes. The outer sheath of the nerve, which is continued into the sclerotic, comes from the dura through the optic foramen. It is therefore, of course, attached to the edges of that opening, and also at the same place to the periosteum lining the orbit.

VII.

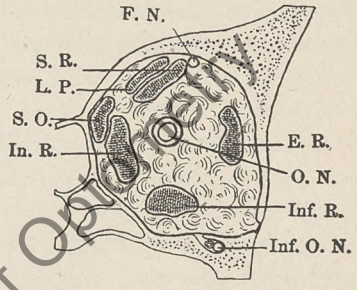
The muscles inside the orbit are the levator palpebræ superioris, the four straight, and the superior and inferior oblique muscles. All except the last-named arise near the optic foramen. The origin of the four recti has been variously described with very unnecessary complications. They spring in common from a short tendinous tube which includes the optic foramen and the inner part of the sphenoidal fissure. It therefore is oval on section, the long diameter being placed transversely. It springs from the edges of the optic foramen on its inner side and above, inseparably connected with

Fig. 26.



Frontal frozen section of left orbit, seen from before, about twelve millimetres behind globe.—*S. R.*, superior rectus; *L. P.*, levator; *S. O.*, superior oblique; *In. R.*, internal rectus; *Inf. R.*, inferior rectus; *E. R.*, external rectus; *O. N.*, optic nerve; *F. N.*, frontal nerve; *Inf. O. N.*, infra-orbital nerve; *6th*, sixth nerve.

Fig. 27.



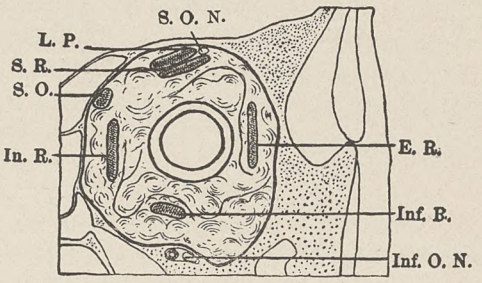
Section about five millimetres behind globe. Letters as in preceding figure.

the sheath of the optic nerve, giving origin to the internal and superior recti. Below, it passes from under the foramen transversely outward across the sphenoidal fissure, giving origin to the inferior rectus. The external rectus springs from the outer border of the fissure and then from a fibrous band which crosses it again, having its lower attachment to the spine (Figs. 1 and 6), usually found on the outer border of the fissure. The upper part of the external rectus is continuous with the outer border of the superior rectus. In fact, the edges of these four muscles are continuous along this fibrous band. When the origin of the external rectus is dissected

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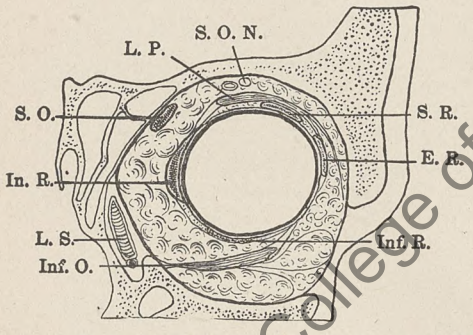
thoroughly from the outside, the fibrous band crossing the fissure and arching over the third nerve gives the muscle the appearance of springing from either side of the fissure; hence it is usually called two-headed, but this is improper, for the muscular fibres arise in an unbroken series, or at least any gap between them is filled by membrane. The levator arises just above the inner part of the superior rectus, somewhat overlapping it to that side. Very near it, but lower, inside the upper part of the internal rectus, arises the superior oblique. Having given the origin of these muscles, we leave them to return to the recti, which form part of a muscular cone, outside of which lie the others. The fibrous ring from which they arise sends tendinous fibres into the ocular side of the muscles. On the outer aspect they speedily become muscular. They are composed of straight parallel fibres with very little connective tissue between them. The muscular bellies soon reach their greatest thickness, and, as is well shown in Fig. 26, they occupy much of the space of the orbit near the apex. Fig. 27, near the back of the eye, shows some of them smaller. Fig. 28, through the posterior portion of the globe, shows them much reduced in thickness and more separated. In Fig. 29 they are still outside of the capsule of Tenon and becoming tendinous. The fibrous tissue forming the sheaths becomes more delicate as they pass forward. The relations of these muscles may be followed on the frontal sections (Figs. 26 to 29) and also on the sagittal sections (Figs. 18 to 21). Certain very important expansions from the sheaths will be considered later. The muscles, having become tendinous, perforate or, more properly, invaginate the capsule of Tenon, and, passing under the conjunctiva, are inserted into the sclerotic at from 5 to 8 millimetres from the cornea. The recti differ among themselves in many respects: in size, in the length of the anterior tendon, in its breadth at the line of insertion, and in the distance of this line from the cornea. These points are shown in the following table, compiled from Volkmann, Merkel, and Fuchs:

FIG. 28.



Section about three millimetres in front of back of globe. Letters as before.—*S. O. N.*, supra-orbital nerve.

FIG. 29.



Section near equator of globe. Letters as before.—*Inf. O.*, inferior oblique; *L. S.*, lacrymal sac.

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	Weight of Muscle.	Length of Tendon.	Breadth at Insertion.	Distance from Cornea.
Authority	Volkmann.	Merkel.	Fuchs.	Fuchs.
	Gramme.	Millimetres.	Millimetres.	Millimetres.
Internal rectus	.747	8.8	10.3	5.5
Inferior rectus	.671	5.5	9.8	6.5
External rectus	.715	3.7	9.2	6.9
Superior rectus	.514	5.8	10.6	7.7

It is needless to say that in several of these respects the variation is considerable. It is worth noting that the rectus internus is the heaviest (presumably, therefore, the strongest) muscle, and that being attached nearest to the cornea it has a decided mechanical advantage. The superior is both the weakest and the worst placed. It appears from the last column of the above table that the insertions of the recti may be diagrammatically represented by thickenings on a spiral line round the cornea, which, starting at 5.5 millimetres from its inner border, passes downward and outward, upward and inward, gradually receding from it. There is, of course, much individual variation. Fuchs found no difference in the distance of insertion between normal and myopic eyes, but the breadth of the line of insertion is, on the average, greater in the latter. As a rule, whether inserted nearer or farther, the muscles retain their relative distances. According to Fuchs, the greatest irregularity is in the inferior and external recti, which are often at the same distance. In a number of measurements made for this work it was found that the external and superior were about the same distance from the cornea at a point about half-way between Fuchs's figures,—that is, from 7.1 to 7.3 millimetres. Merkel's measurements agreed with those of Fuchs for the inferior and external, but he found the internal and inferior more distant from the cornea. Fuchs's results deserve to remain the standard ones, but it is clear that there is a good deal of irregularity. The lines of insertion are not parallel to the edge of the cornea. The superior has the end of its inner edge much in advance of the other, and most of its insertion is usually on the outer half of the eye. The inferior, though more symmetrical, has its outer end a little in front. There is a considerable amount of loose connective tissue between the eyeball and the insertions of the tendons and also at their sides, so that it requires dissection to ascertain the precise position of their borders. As the axes of the orbits diverge considerably, while the axes of the eyes are parallel, it is easy to see that both the superior and inferior recti, being inserted far in front of the equator, must, in addition to the obvious action of either, turn the eye inward. At the same time they probably cause a certain amount of rotation, the superior rolling a point on the upper border of the cornea inward and downward, the inferior rolling it outward and downward. Evidently peculiarities in the insertion of one of these muscles must affect the range and direction of these movements. The internal and external recti move

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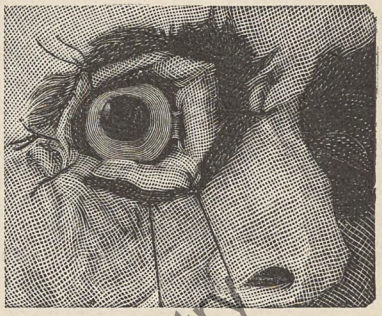
the pupils directly inward or outward. The origin of the superior oblique muscle has been given. It quickly gets into the upper inner part of the orbit (Fig. 33), lying well outside the cone formed by the four recti, becomes a small round fibrous band as it plays through the pulley, and then expands into a tendon which, passing backward and outward between the globe and the superior rectus, is inserted as follows. The anterior point of the line of insertion lies about as far outward as the outer end of the superior rectus, and is about as far behind the equator as the latter is before it. From this point the line, according to the more usual arrangement, runs in a curve backward and inward, to end on the inner side of the meridian. In certain cases it runs more directly backward, being throughout its course external to the meridian. In the former class the line of insertion approaches the direction of the equator, in the latter that of the meridian. Either form may be found in a normal or in a myopic eye, but the latter is essentially that of the myopic. The breadth of the insertion ranges from 6.8 to 14 millimetres, being narrower on the average in myopic eyes (Fuchs). The inferior oblique springs from the floor of the orbit just inside the opening for the nasal duct. It is almost entirely muscular. Passing between the floor of the orbit and the inferior rectus, it curls round the globe, to be attached far back in the outer and inferior region of the back of the eye. The distance of its insertion from the outer sheath of the optic nerve averages 5.2 millimetres for normal eyes and 7.1 for myopic ones. In the former the breadth of the insertion is 9.4 millimetres, in the latter, 10.5 millimetres. The superior oblique as a factor in the movements of the eye must, for obvious mechanical reasons, be supposed to start from the pulley. Thus the two obliques practically leave the upper and lower inner angles of the base of the orbit and pass backward and outward to the posterior outer portion of the globe. Each oblique turns the pupil outward. The superior, in addition, turns it downward and rotates (a point at the top of the cornea) inward. The inferior turns it upward and rotates outward. It is customary to teach that the inferior oblique corrects the effect of the obliquity of the superior rectus, so that, both acting together, the eye is turned straight upward, while the inferior rectus and the superior oblique turn it straight downward. Theoretically this is tolerably certain, but practically it is to be remembered that it is very unlikely that one or even two of these muscles ever act alone. The accuracy of any movement is due not alone to the pull of the muscle to which it is usually ascribed, but also to the graduated resistance of the antagonists. Probably the simplest movement of the eye is made by the more or less active concurrence of all the muscles. The levator palpebræ superioris runs close above the inner portion of the superior rectus. The areolar tissue between them is so slight that transverse vertical sections show them in the back part of the orbit almost as one muscle. Anteriorly they are quite distinct, as the rectus (except its expansion) sinks to the eye and the levator expands into the broad layer already described, stretching pretty nearly across the roof of the orbit.

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VIII.

The eyeball, from the optic nerve to near the border of the cornea, is enclosed by a delicate membrane, called the capsule of Tenon. As the complications of this membrane are limited only by the perverted ingenuity of those who describe it, let it be understood that in this paper is meant only the capsule around the globe. Near the cornea the conjunctiva and the capsule of Tenon fuse into a single membrane. The arrangement of the capsule may be understood by following the steps of the dissection shown in Fig. 30. A cut with a very sharp knife was made close around the cornea, dividing the membrane formed by the capsule of Tenon and the conjunctiva. This was then turned back from the eyeball by a blunt instrument. The outer canthus was cut to gain room, and the membrane reflected and stitched to the integument. This exposes a cavity between the globe and the membrane. At the free edge, of course, this membrane is made of both conjunctiva and Tenon's capsule, but these two separate within three millimetres from the edge of the cut. What, therefore, is seen on the inside of the reflected membrane is wholly Tenon's capsule. It is shown diagrammatically in Figs. 18 to 21. It is a delicate membrane enclosing a lymph-space between itself and the globe and separating the latter from the fat of the orbit. Bands of connective tissue run through this space. They are particularly numerous in the posterior part. Authorities differ as to the place at which the capsule ends behind. It goes to the optic nerve. Nevertheless, Schwalbe has shown that a lymph-space around the optic nerve can be injected from it. It would seem that this could take place through small openings, especially at the points of entrance of the ciliary vessels and nerves, and that the capsule may be said to reach the optic nerve, as gross appearances indicate. It is taught as by common consent that the capsule of Tenon is a socket in which the eyeball rotates without change of position, except, perhaps, that under certain circumstances it may move a minute distance forward or backward. Anatomy shows that this is impossible. It is easy to see that as Tenon's capsule is closely attached to the globe near the cornea, it is out of the question that the former should stand still while the latter moves in it. Undoubtedly the two move together on the cushion of fat behind them, and perhaps some slight motion may occur between them. The muscles pierce or, more properly, invaginate this membrane. The folds shown in the figure at their points of passage through it are caused by its position as dissected.

Fig. 30.



Dissection of capsule of Tenon, by Dr. Tenney.

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From the fibrous tissue forming the sheaths of the recti strong expansions pass off before the muscles pass through the capsule of Tenon. Those of the superior and inferior recti have been described with the lids. Analogous but stronger ones pass off laterally not only to the bones of the base of the orbit, but to the angles of the lids and the conjunctiva. The external one goes also to the so-called external palpebral ligament, and the inner goes also to the reflected tendon behind the tear-sac (Fig. 25). These not only admit of dissection, but are beautifully shown on frozen sections. Although the fibrous tissue of the sheaths of the muscles is undoubtedly continuous with that of the capsule of Tenon, it seems unnecessary to make them expansions of the latter, as is done by Sappey and others. Fig. 25, though somewhat diagrammatic in execution, is from an actual section, and gives a true representation of the fibres. A similar view is to be found in Von Gerlach's work. Almost all other writers represent these expansions as nearly transverse bands passing more to the walls of the orbit than to the soft parts. The effect of these expansions is partly to steady the eyeball and to resist the backward pull of the recti, partly to draw the lids and the fold of the conjunctiva in harmony with the movements of the eye (Fig. 12). Quite a strong fascia covers the tendon of the superior oblique from the globe to the pulley. Besides these, Lockwood has described a hammock-shaped sling of fibrous tissue more or less connected with the capsule and with other processes of orbital fascia, which, fastened at either side of the orbit, supports the globe. It is best seen when dissected from below.

The orbit is filled with fat, which is bounded in front by the capsule of Tenon and the fibrous expansions. The fat of the orbit deserves special notice. It is not all of the same kind. Inside the space bounded by the muscular cone, and in front by the capsule of Tenon enclosing the eye, the fat is very delicate and loosely packed, especially around the optic nerve and the delicate ciliary vessels and nerves. Frozen sections, when fresh, show in many places most delicate fasciæ dividing the fat. Both transverse and longitudinal sections show a thin irregular membrane at some distance, say from three to ten millimetres, from the optic nerve bounding Schwalbe's supra-vaginal space. It may be doubted whether this constitutes an absolutely continuous tube. It may also be doubted whether it entirely limits this most delicate fat which forms an almost fluid support for the eye, well adapted for its movements. At certain places in the orbit the fat is very different, being collected into large and comparatively hard masses. One of these extends from the inside of the lacrymal gland to the posterior surface of that organ, another is in the lower part of the front of the orbit. It probably helps to make the prominence of the lower lid which is so striking when the eye is turned upward. In frozen sections lines of thin fascia are seen cutting off these and similar collections. There is also fat of various degrees of density between these two extremes.

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IX.

The ophthalmic artery arises inside the skull from the internal carotid just after that vessel has pierced the dura. It passes into the orbit through the optic foramen below and to the outer side of the optic nerve. If we remember that the outer sheath of the optic nerve is continuous with the dura along the margin of the optic foramen, it is clear that at first the artery must lie within the sheath. It leaves it very soon, running between the nerve and the beginning of the external rectus; then curving forward and inward to run nearly transversely, it crosses over the nerve below the superior rectus and reaches the upper inner angle[1] of the orbit far back. It then runs forward below the superior oblique, perforates the upper lid below the trochlea, and divides into the nasal and frontal arteries. As Sappey remarks, its branches may be divided into three sets, —those going to the globe, those of the appendages, and those which merely pass through the orbit to go elsewhere.

The first class comprises the central artery of the retina and the ciliary arteries; the second, the branches to the muscles, the lacrymal apparatus, and the lids; the third, the terminal branches and the ethmoidal arteries. Be it noted, however, that the anterior ciliaries come from branches of the second set. There are usually two ciliary arteries, an outer and an inner, each of which divides into many branches which pierce the sclerotic near the optic nerve. The number of these secondary branches may reach twenty, but this is uncommon. Two, called the long ciliaries, after entering the globe, run to the anterior part of the eyeball, but they are not easy to distinguish from the other branches while in the orbit, though said to be larger. The anterior ciliary arteries, some half-dozen in number, are twigs of the muscular branches and perhaps of the lacrymal and supra-orbital, which, having divided once or twice, pierce the sclerotic in a ring near the margin of the cornea. The two posterior ciliaries and the central artery of the retina are the first branches of the ophthalmic. According to Meyer,[2] who has written a very valuable paper on the orbital arteries, the normal arrangement is for the central artery and the inner of the posterior ciliaries to arise in common, very often within the sheath of the optic nerve, while the outer one arises a little later. The central artery pierces the nerve within 1.5 centimetres of the globe. The next branch is the lacrymal, which arises from the outer side of the vessel to run forward to the gland along the upper border of the outer rectus. It supplies by its terminal branches the outer part of the lids and of the conjunctiva, anastomosing with arteries of the face. It has an important connection soon after its origin with a branch from the middle meningeal which enters the orbit through the sphenoidal fissure. The importance of this lies in the changes in the plan of

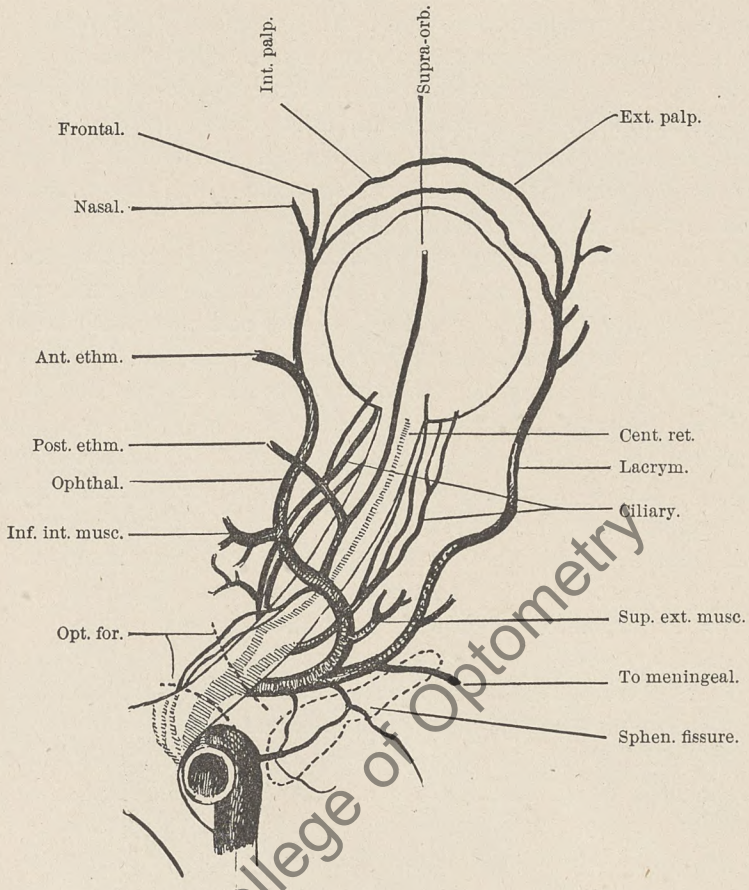
[1] The word "angle" is used for convenience. Sections show that the term is inexact as expressing the shape of the orbit.

[2] Morphologisches Jahrbuch, Bd. xii., 1887.

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the orbital arteries which may spring from an early variation in the course of blood through this system. This may lead to the lacrymal arising from the middle meningeal, or, more important still, to the ophthalmic becoming a branch of that artery and reaching the orbit through the fissure, or through a special canal. The muscular branches, two or three in number, are pretty uncertain in their mode of origin. The supra-orbital, which is neither constant nor important, runs in the upper part of the orbit at first to the inner

FIG. 31.



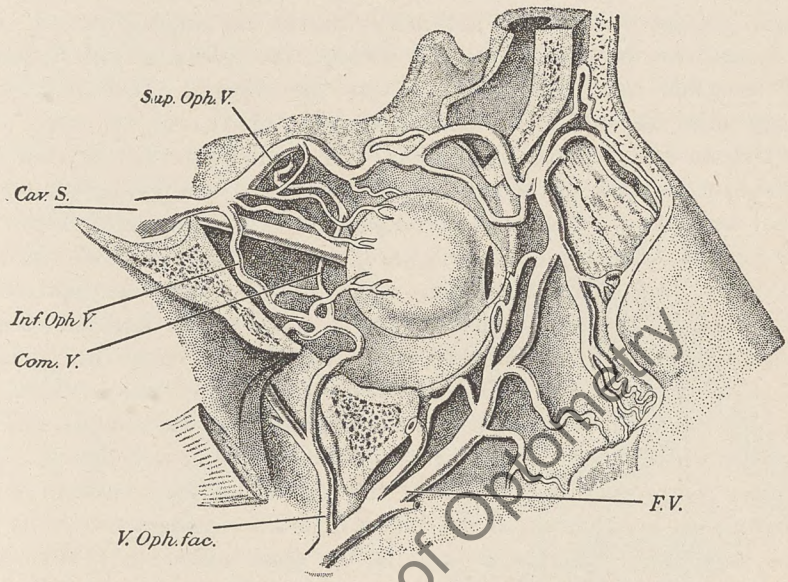
The orbital arteries. (From Quain's Anatomy, after Meyer.)

side of the levator palpebræ and then above it to the supra-orbital notch. The two ethmoidal arteries leave the orbit by the little ethmoidal foramina between the frontal bone and the os planum of the ethmoid; the posterior may be a branch of the supra-orbital, the anterior comes from the main trunk. The palpebral branches have been described with the lids. It remains only to state that they may arise either separately or in common, and pass out of the orbit above the internal palpebral ligament. Meyer gives

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the following as the order of the origin of the branches of the ophthalmic artery: 1, the retinal artery with the inner ciliary; 2, outer ciliary; 3, lacrymal; 4, upper and outer muscular; 5, supra-orbital with posterior ethmoidal; 6, inner and lower muscular; 7, anterior ethmoidal; 8, final division into palpebral, frontal, and nasal. Variations of the lacrymal artery have been discussed. The other important variation is of the course of the ophthalmic itself, which sometimes passes under the optic nerve instead of over it. The arteries of the orbit are tortuous and but lightly connected with the fat of the orbit, so that it is easy for them to yield to the varying pressure depending on the swelling of the muscles, on the movements of the globe, or on increased pressure from the heart or increased resistance from distended veins.

FIG. 32.



Veins of the orbit. (From Sesemann.) *Cav. S.*, cavernous sinus; *Com. V.*, communicating branch between *Sup. Oph. V.*, superior ophthalmic vein, and *Inf. Oph. V.*, inferior ophthalmic vein; *F. V.*, facial vein; *V. Oph. fac.*, ophthalmo-facial vein passing through spheno-maxillary fissure.

The veins of the orbit form a very free system of anastomosing vessels between the sinus cavernosus inside the skull, the facial vein on the surface of the face, and the tributaries of the internal maxillary through the spheno-maxillary fissure. It seems reasonably certain that the blood from the lids returns by the superficial veins, that the blood from the eyeball returns through the sinus cavernosus, and that most of the blood in the orbit can in case of need flow either into the sinus or into the superficial or deep veins of the face. We incline to the opinion that under ordinary circumstances the general current is inward. The chief vein of the orbit is the superior ophthalmic, which begins at the upper inner angle of the orbit by communicating branches with the frontal and nasal veins. It runs

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backward across the optic nerve, under the superior rectus, through the sphenoidal fissure, to the cavernous sinus. The vein may enter the sinus on either side of the external rectus. Most writers ignore this point, and the statements of others do not agree. We incline to the opinion that the vein usually passes inside of the rectus. This vein presents a remarkable narrowing just before its end, and sometimes a considerable dilatation near the middle. According to Sesemann,[1] it has no valves, though each of its tributaries has a valve at the point of entrance. Its contents, therefore, can escape in either direction. It has, moreover, constant connections with the inferior ophthalmic vein by a small communicating branch (*Com. V.*, Fig. 32). The inferior ophthalmic vein, which is much smaller than the preceding, runs near the floor of the orbit above the inferior rectus to the cavernous sinus, or sometimes to a vein called by Hyrtl the ophthalmo-meningeal. It begins at the front of the orbit by a plexus about the inferior oblique which drains the inferior part of the conjunctiva. It communicates with the veins of the face through the spheno-maxillary fissure. The lacrymal vein opens usually into the superior ophthalmic by a branch called the ophthalmo-facial, taking the blood from the upper conjunctiva as well as from the gland. The smaller veins of the orbit correspond in the main to the arteries, and, with two exceptions, call for no special description. The venæ vorticosæ, four or five in number, leave the orbit near its equator and pass backward, becoming the ciliary veins, to open into one or both of the ophthalmic veins. The question has been raised as to whether they are compressed by the action of the muscles. Fuchs describes them as in two pairs, an upper and a lower, each with an inner and an outer vein. He finds that the recti exert no action on them, but that one upper and one lower may be compressed by the oblique muscles, especially when the eye is in the position for looking at near objects. The alternate compression and release of the veins help the circulation of the eyeball. The central vein of the retina deserves consideration for its obvious importance. At first it runs in the optic nerve, but it reaches its outer side about half-way back. It soon pierces the sheath and runs to the sinus cavernosus. Whatever suction may occur in the sinus is therefore easily felt by the blood in this vein. Sesemann insists on the point that the central vein has always at least one side branch. The most common connection is with the superior ophthalmic. Indeed, this branch may be so large as to make it doubtful into which the vein may be said to empty. This provides an escape for the blood of the retina in case of thrombosis of the sinus. Sometimes this vein runs into a delicate plexus around the optic nerve.

The lymphatic circulation of the orbit proper is partly through vessels and partly through spaces. The vessels are said to be few. They pass through the spheno-maxillary fissure to the deep facial glands, a small group by the back part of the buccinator and the side of the pharynx.

[1] Archiv für Anatomie und Physiologie, 1869.

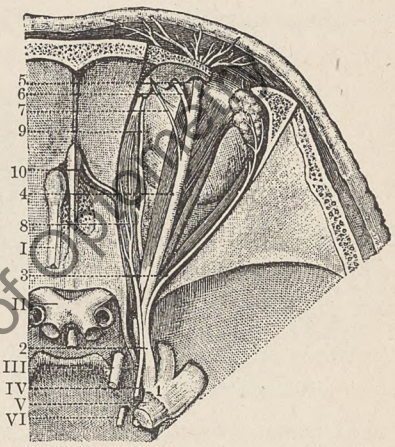
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The spaces through which lymph passes are Tenon's capsule and the lymph-space around the optic nerve into which it drains (Schwalbe's supra-vaginal space).

X.

The nerves of the orbit are the third, fourth, and sixth pairs, the first division of the fifth pair, and some sympathetic fibres from the cavernous plexus. Besides these, but hardly belonging to this subject, may be mentioned the infra-orbital while in its groove, and the orbital branch of the superior maxillary, which enters the orbit through the spheno-maxillary fissure to divide into the temporal and malar branches, which leave the orbit through their respective minute canals in the malar bone. According to Sappey, it gives another branch running to the lacrymal gland and to the outer angle of the lids. The nerves of the orbit enter it through the sphenoidal fissure, but on or before reaching it the third divides into an upper and a lower division, and the fifth into the lacrymal, frontal, and nasal. They pass through the fissure as follows: most externally and highest the lacrymal, then the frontal, and then the fourth, these three being external to the outer rectus. Internal to that muscle, and therefore entering the cone formed by the recti, come the others. The upper division of the third passes highest. Below it comes the nasal, then the lower division of the third and the sixth on about the same level, the sixth being external. The sympathetic filaments do not seem to be very regular in their entrance. They are, at all events, near the nasal nerve. The division of the third pair occurs at just about its entrance into the orbit. The upper division, which is the smaller, supplies the superior rectus and the levator. The branch to the former enters the muscle on its lower side, that to the latter passes to the inner side of that muscle (sometimes through it) to the under surface of the levator. The larger lower division, passing downward, gives branches to the inferior and internal recti, which enter them through their superior and external surfaces respectively. The longest branch is to the inferior oblique, which it enters from below. This gives off at its origin the short, motor root of the lenticular ganglion.

FIG. 33.



Nerves seen from above. (From Sappey, after Hirschfeld.) The Roman numerals indicate the cranial nerves of the corresponding numbers. 1, Gasserian ganglion; 2, first division of fifth pair; 3, lacrymal; 4, frontal; 5, supra-orbital; 6, branch of same; 7, supra-trochlear; 8, nasal; 9, infra-trochlear; 10, nasal, after leaving the orbit.

The fourth nerve passes above the optic nerve to the superior oblique, which it enters from above in several branches.

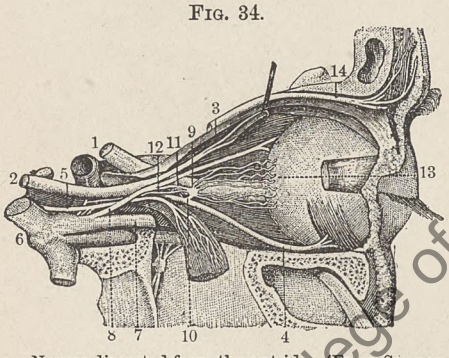
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The sixth nerve has a short course in the orbit. It at once reaches the inner side of the external rectus, and soon breaks up into many branches which enter that muscle (Fig. 34).

There are certain points which the nerves of the recti have in common worthy of mention. They are all very large in proportion to their muscles. The external rectus probably receives relatively to its size the largest nerve in the body. The nerves all break up into a sheaf of diverging branches before entering the muscles, and finally each enters its muscle on the side nearest to the optic nerve.

The three branches of the first division of the fifth pair are, of course, purely sensory. The frontal nerve runs close against the periosteum of the roof of the orbit. At about the middle of the orbit it gives off the supra-trochlear, which reaches the upper inner angle of the base of the orbit, where it sends a twig to the infra-trochlear branch of the nasal and leaves the orbit. Its distribution to the lids and conjunctiva has been described. Beyond the origin of the supra-trochlear the frontal changes its name to the supra-orbital, which passes through the notch or foramen, dividing either before or after its passage into two chief branches. The lacrymal nerve (Fig. 33), which enters higher and more externally than any other, gains at once the upper and outer part of the orbit and runs above the external rectus to the gland which it supplies. Before reaching the gland it sends down a communication to the orbital branch which enters through the spheno-maxillary fissure. The lacrymal supplies also a part of the conjunctiva and ends in the upper eyelid. The nasal branch (Fig. 34), which the Germans more happily call the naso-ciliary, passes into the orbit between the muscles much lower than the two preceding. It is at first external to the optic nerve and at a lower level, but it passes upward and inward, crossing over the nerve below the superior rectus to the inner wall of the orbit, which it leaves by the anterior ethmoidal foramen, going beneath the superior oblique muscle. In the early part of its course, while still outside of the optic nerve, it sends the long root to the lenticular ganglion. After crossing the optic nerve one or two long ciliary filaments pass from it to the eyeball. Before leaving the orbit it sends off the infra-trochlear nerve, an important branch which supplies the lacrymal sac, the conjunctiva, the lids, and a bit of the nose, leaving the

FIG. 34.



Nerves dissected from the outside. (From Sappey, after Hirschfeld.) 1, optic nerve before entering the optic foramen; 2, third pair; 3, branch of same to levator and to superior rectus; 4, branch of same to inferior oblique; 5, sixth nerve to external rectus, which is turned down; 6, fifth nerve; 7, first division of same; 8, nasal nerve, branch of preceding; 9, lenticular ganglion; 10, short, motor root of same; 11, long, sensory root of same; 12, sympathetic root of same; 13, ciliary nerves; 14, supra-orbital branch.

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orbit above the internal palpebral ligament. The main nerve, after leaving the orbit, passes for a short distance through the cranial cavity and then plunges into the nose, supplying a part both of the mucous membrane and of the skin. It is often mentioned in explanation of reflexes passing between eye and nose. The lenticular ganglion (Fig. 34) is diagrammatic in its simplicity. It has a short root (motor) from the third, springing from the branch to the inferior oblique, a long root (sensory) from the nasal, and one or two long sympathetic fibres from the cavernous plexus. It is situated very close to the optic nerve on its outer side, rather below than above it, at one-third (or a little more) of the distance from the foramen to the globe. It is irregular in size and shape, its diameter being some two or three millimetres. The short ciliary nerves which spring from it tend to be divided into an upper and a lower group. The number of primary nerves as well as the number of branches they break up into is very variable. If we may believe all the statements, the latter range from ten to twenty. They pierce the sclerotic with the ciliary arteries in a circle round the optic nerve.

XI.

If the contents of the orbit be examined from above by breaking and removing the pieces of the roof, one is struck by the looseness of the attachment of the periosteum which remains intact covering the soft parts. The frontal nerve and its continuation, the supra-orbital, are immediately below it and easily seen through it. At the same level, but less evident, are, towards the inside, the supra-trochlear branch running near the outer border of the superior oblique in the front part of the orbit, and in the back part the fourth nerve running above the same muscle. At the outside of the orbit the lacrymal nerve runs above the external rectus along the wall. The lacrymal artery is very near this nerve, but the supra-orbital artery arises from the ophthalmic within the cone of muscles (or after its main continuation has passed out of it to the inside of the superior rectus), so that it does not reach the roof in the posterior part of the orbit. The main artery, lower than the nerve, is against the upper part of the inner wall, in the anterior half, or rather more, of the orbit. The veins of the same names as these arteries have the same general course. In the upper outer angle of the base the lacrymal gland lies beneath the periosteum, enclosed in its sheath. Beneath these structures lies the levator palpebræ superioris, narrow behind and closely attached to the subjacent superior rectus. Farther forward its muscular belly lies somewhat internal to that of the latter; but its expansion spreads anteriorly across the orbit, mingling with transversely placed fibres to form Müller's muscle, which sinks into the lid and partially divides the lacrymal gland. At the top of the inner wall of the orbit runs the superior oblique. At the inner wall are the ethmoidal arteries and veins, the nasal nerve passing through the anterior ethmoidal foramen and its infra-trochlear branch. Almost all the space

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near the apex of the orbit is taken up by the recti forming a cone round the optic nerve. As they diverge they leave room for much fat, through which pass the ciliary arteries and nerves and the continuations of the venæ vorticosæ of the eyeball. The artery, at first below and then outside of the nerve, passes over it, as does also the nasal nerve. The ophthalmic vein is in this cone beneath the superior rectus, and the inferior ophthalmic vein below the optic nerve. The third pair, the sixth, and the nasal nerve pass at once from behind into this cone. The ophthalmic veins, or the single one formed by their union, leave the cone to pass into the sinus. Below the globe lie the inferior oblique and Lockwood's suspensory ligament of the eye.

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THE ANATOMY OF THE EYEBALL AND OF THE INTRA-ORBITAL PORTION OF THE OPTIC NERVE.

BY FRANK BAKER, M.D., PH.D.,

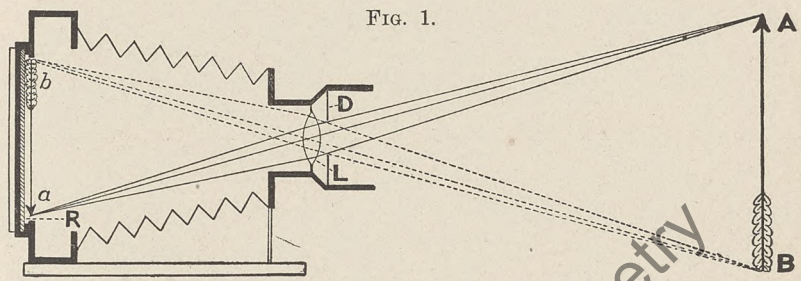
Professor of Anatomy, University of Georgetown, Washington, D.C., U.S.A.

THE EYEBALL.

GENERAL CHARACTERS.

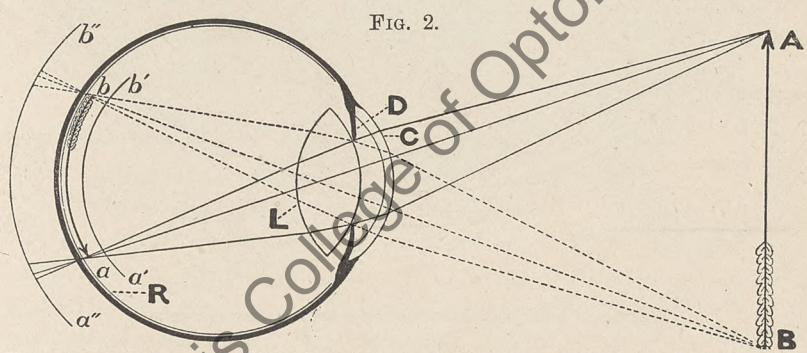
THE eyeball[1] is a spheroidal body situated in the anterior portion of the orbit and attached to the brain by a stem-like structure called the optic

FIG. 1.



Camera obscura of a photographic apparatus.—*AB*, object; *D*, diaphragm for shutting off too divergent rays; *L*, lens for refracting the rays so that they will form the image *ab* upon the sensitive plate *R*.

FIG. 2.



The eye as a camera.—*AB*, object; *C*, cornea, where the rays undergo a first refraction; *D*, the iris, that acts as a diaphragm for shutting off too divergent rays; *L*, lens, where the rays are again refracted; *R*, retina, upon which the image *ab* is projected; *a′b′* represents the surface of a hypermetropic eye, and shows that the rays are not completely focussed, and consequently the image must be blurred and indistinct; *a″b″* represents the surface of a myopic eye, and shows a similar condition.

nerve. It consists of three concentric envelopes, known as the coats or tunics of the eye, which enclose certain transparent contents, the whole

[1] Syn.: globe of the eye; apple of the eye; *bulbus oculi*.

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forming a dark chamber or *camera obscura* like that of a photographic apparatus, in which the light from any object within its field is by refracting media thrown upon a background so placed that the rays diverging from any given point converge to the corresponding point of a small inverted image. (Figs. 1 and 2.)

The external coat (see Fig. 3) is composed of condensed, fibrous con-

FIG. 3.

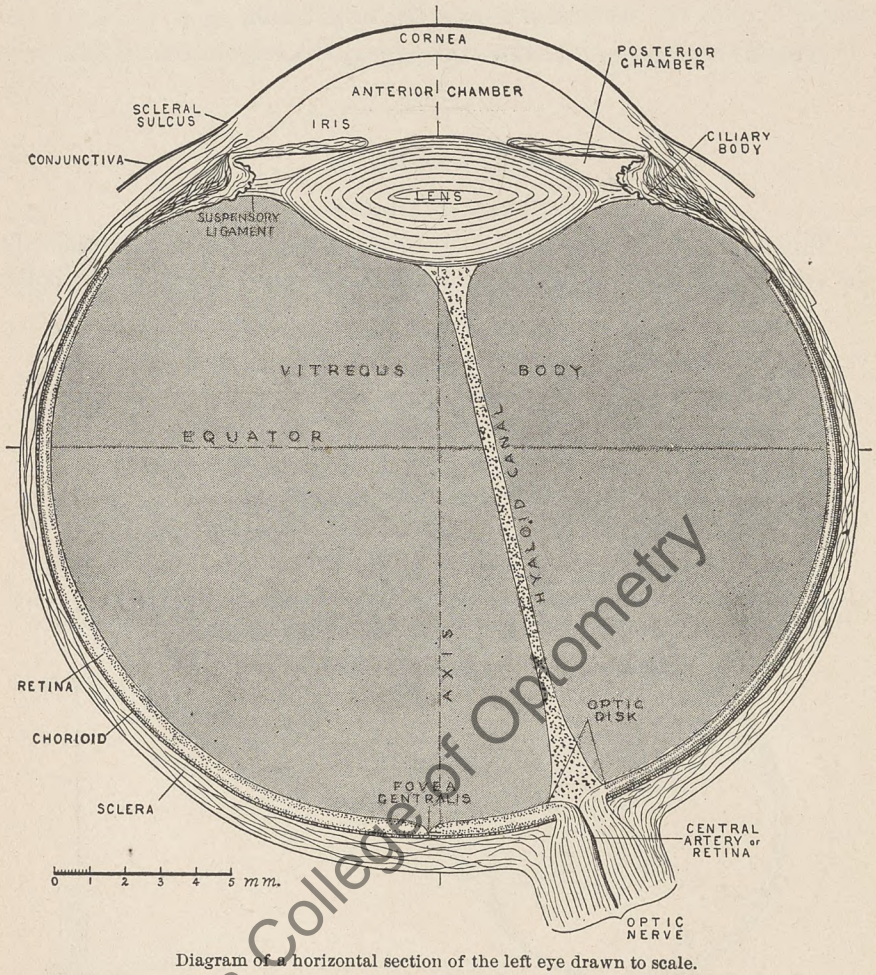


Diagram of a horizontal section of the left eye drawn to scale.

nective tissue which by its resistance to internal pressure gives shape to the eye; its posterior portion, comprising about five-sixths of the whole, is white and opaque, and is known as the *sclera;* its anterior one-sixth is clear and transparent, and is called the *cornea.*

The middle coat is essentially vascular, and serves as a nutritive organ for the other coats. It also contains pigmented cells that prevent reflections within the cavity of the ball, as well as plain muscle-fibres that serve for

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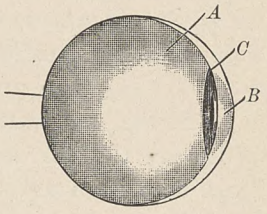
adjusting the apparatus of vision. Its posterior part is known as the *chorioid*, its anterior part—where it forms a delicate curtain pierced by an aperture, the pupil—as the *iris*.

The inner coat is essentially nervous in character, being an outgrowth from the brain and containing the ganglionic elements that supply the optic nerve. It is known as the *retina;* upon it the rays of light are concentrated, and by the action of its cells the sensations of vision are set in train.

The spaces within the globe are occupied by fluid or semi-fluid contents, and are known as the *chambers* of the eye. Two principal compartments are established by the interposition of a transparent lenticular structure called the *crystalline lens*, which is placed transversely across the globe, just behind the pupil. The space in front, which is filled with a watery fluid, —the *aqueous humor*,—is called the *aqueous chamber;* that behind, occupied by a soft and jelly-like material,—the *vitreous humor*,—is the *vitreous chamber*. During a considerable part of fœtal life the aqueous chamber is divided by a vertical transverse partition composed of the iris and a delicate sheet—the pupillary membrane—stretched across the site of the future pupil. These subdivisions are known as the *anterior* and *posterior chambers*. When the pupillary membrane disappears, as it usually does before birth, they communicate through the pupil.

The terms usually applied to a spheroid are often used in describing the eye. The *axis* is the antero-posterior diameter passing through the summit of the cornea. For purposes of precision that part of this diameter between opposite points of the internal surface of the capsule is termed the *internal* axis, the entire diameter being then known as the *external* axis. The points where this axis cuts the surface are termed *poles*, distinguished as anterior and posterior. The *equator* is the great circle equidistant from the poles, and the *meridians* are great circles passing through both poles.

FIG. 4.



The eyeball compared to a sphere.—*A*, sclera; *B*, cornea; *C*, scleral sulcus.

In popular language the eyeball is considered as a globe, and when we reflect that its external coat is a capsule in a state of tension over fluid or semi-fluid contents, it would seem natural that this should be the shape assumed. Yet on examining its dimensions closely it is found to be by no means exactly spherical. The principal muscles that move the ball are inserted upon the capsule by tendinous thickenings arranged about the region where the sclera and the cornea join. This causes a distinct change in the curvature at this place, with the formation of a slight groove, the *scleral sulcus*.[1] This change of curvature occasions an apparent projection of the cornea beyond the limits of the

[1] Syn.: *sulcus sclerœ; sulcus sclerœ externus* (Schwalbe).

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larger sphere. The latter would, however, if continued, enclose the whole of the cornea, as shown by the diagram, Fig. 4. Any increase of intra-ocular pressure diminishes the convexity of the cornea and tends to obliterate this groove.

The eyeball also shows other slight deviations from the spherical form, and these are by no means easy to determine with precision, as may be judged from the fact that some of the most recent anatomical works differ in their statements as to which diameter of the eye is the greatest. The following citations from principal treatises on anatomy show variations of statement on this subject:

	Antero-Posterior Diameter.	Transverse Diameter.	Vertical Diameter.
	Millimetres.	Millimetres.	Millimetres.
Quain's Anatomy, 10th edition, 1894	24	24.5	23.5
Gray's Anatomy, 13th edition, 1893	22.9	25.4	22.9
Morris's Anatomy, 1894	24.5	23.9	23.5
Macalister's Anatomy, 1889	24.27	24.25	23.65
Leidy's Anatomy, 1889	25.4	25.4	25.4
Testut, Anatomie Humaine, 1894	25.26	23.5	23
Debierre, Anatomie de l'Homme, 1890	24	23.5	23
Rauber, Anatomie des Menschen, 1893–94 (Cites the older work of Krause.)	24.27	24.32	23.6
Gerlach, Specielle Anatomie des Menschen, 1891	24.2	23.8	23.5
Vierordt, Daten und Tabellen, 1893	24	24.3	. .
Merkel, Topographische Anatomie, 1887	24.3	23.6	23.3

These variations probably arise from the fact that the eyes measured were not all in a perfectly fresh condition, and that the changes due to age were not always properly considered. Evaporation of the fluid contents of the eyeball commences at once after death, and soon removes a sufficient quantity to make a perceptible difference in the tension of the coats and consequently in the measurement of the diameters. Differences in manipulation have doubtless some effect, as if the ball is left to lie for any time upon a hard surface it becomes flattened sufficiently to affect the measurements. Among the most careful determinations recorded are those of Sappey, who measured a large number of eyes belonging to both sexes and various ages. He has published the table given on the following page comprising certain selected cases considered as normal. Finding that in the great majority of cases the dimensions of the right and left eyes did not sensibly differ in the same subject, he used but one eye of each.

The table shows that the eyeball may properly be described as an ellipsoid, flattened slightly from above downward and from side to side. For practical purposes the antero-posterior, or longest, diameter may be considered as about twenty-four millimetres (nineteen-twentieths of an inch), while the vertical, or shortest, is about one millimetre less, and the transverse is midway between the other two.

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DIMENSIONS OF THE EYEBALL.

FEMALES.

No.	Designation of Eye.	Age.	Antero-Posterior Diameter.	Transverse Diameter.	Vertical Diameter.	Internal Oblique Diameter (from below inward).	External Oblique Diameter (from below outward).	Distance from Optic Nerve to Internal Side of Cornea.	Distance from Optic Nerve to External Side of Cornea.
1	Right	18	23.0	23.2	23.0	23.4	23 4	26	33
2	Right	25	23.4	22.8	22.5	23.3	23.3	25	32
3	Left	28	24.0	23 3	23.3	23.5	23.8	26	33
4	Right	30	23.5	22.6	22.6	24.1	23.8	26	34
5	Left	35	23.9	23.1	23.1	23.7	23.7	28	33
6	Left	40	25.0	23.6	23.6	24.3	23.7	29	34
7	Right	50	24.3	23 8	24.0	24.6	25.1	27	33
8	Left	66	26.4	27.1	23.4	25.7	25.3	32	37
9	Left	69	23.6	23.5	23.0	25.4	25.3	28	33
10	Left	72	22.9	22.8	22.3	23.5	23.6	27	34
11	Left	74	23.4	23.3	22.6	23.8	23.3	28	32
12	Left	81	23.2	22.5	22.5	23.1	23.4	25	31
Average Dimensions.			23.9	23.4	23.0	23.8	23.8	27.2	33.2

MALES.

1	Right	20	24.8	23.3	23.8	23.7	23.9	28	33
2	Left	22	23.6	22.8	22.5	23.5	23.5	26	33
3	Left	25	24.2	22.4	22.2	23.5	23.6	27	34
4	Right [1]	26	24.3	23.4	23.4	23.7	23.5	27	33
5	Right	31	24.7	25.9	22.8	24.4	24.8	30	37
6	Left [2]	35	26.3	25.4	25.2	. .	.	31	39
7	Left [3]	45	25.2	24.6	24.0	24.8	25.0	29	37
8	Right	50	24.4	23.9	25.8	23.9	24.5	27	35
9	Left	59	25.0	23.8	23.4	24.3	24.3	27	36
10	Left	63	24 0	24.0	24.0	25.5	24.7	28	35
11	Left [4]	67	24.9	24.9	24.0	.	. .	28	34
12	Left	70	24.3	23.1	24.5	24.6	24.0	25	32
13	Left	75	24.8	23.9	23.8	24.6	24.5	27	35
14	Left	79	24.7	23.6	23.6	24.2	24.5	27	35
Average Dimensions.			24.6	23.9	23.5	24.1	24.2	27.5	34.5
Average for both Sexes.			24.2	23.6	23.2	23.9	23.9	27.3	33.8

There is still a small amount of asymmetry not accounted for. On looking carefully at the eyes of a living person, it will be seen that the pupil is placed a little nearer the nasal side. The nasal hemisphere is, in fact, somewhat smaller than the outer or temporal hemisphere, and planes passed through the equator of the lens in either eye do not exactly coincide, but tend to converge at a very obtuse angle towards the median line,

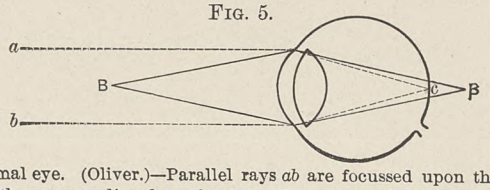
[1] Observed three hours after death.
[2] Observed two hours after death.
[3] Observed four hours after death.
[4] Observed one hour after death.

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and in some individuals below the horizontal plane. The longest equatorial diameters are not horizontal, but oblique.

Individual peculiarities in the dimensions of the eyeball are not infrequent, and may lead to anomalies of vision. Normally the retina is so

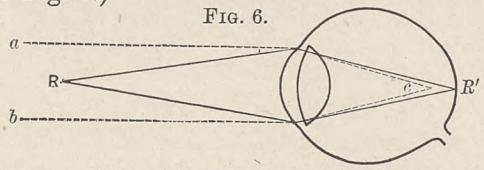
FIG. 5.



An emmetropic or normal eye. (Oliver.)—Parallel rays *ab* are focussed upon the retina, while divergent rays, as those proceeding from the point *B*, come to a focus behind the retina.

placed that the rays of light coming from distant objects, and therefore practically parallel, focus directly upon it when they are refracted by the transparent media at the front of the eyeball, and consequently form a distinct image. (See Fig. 5.)

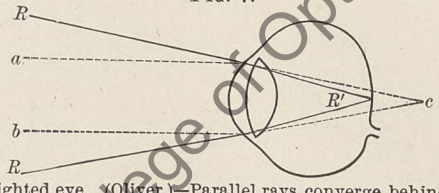
FIG. 6.



A myopic or short-sighted eye. (Oliver.)—Parallel rays converge before reaching the retina. Rays must be *divergent* in order to focus there.

This normal condition is called *emmetropia*.[1] If the axis of the eye is longer than usual, the rays coming from distant objects converge before reaching the retina, and the image appears blurred, while divergent rays from objects near at hand are properly focussed and produce a distinct image. (See the line $a''b''$ in Fig. 2, also Fig. 6.) This is short-sighted-

FIG. 7.



A hypermetropic or far-sighted eye. (Oliver.)—Parallel rays converge behind the retina. Rays must be *convergent* in order to focus there.

ness, or *myopia*.[2] If the axis of the eye is *shorter* than usual, the distant rays focus behind the retina, and a similar blurring of the image occurs, which can be remedied only by the use of a convex lens to make the rays convergent. (See the line $a'b'$ in Fig. 2, also Fig. 7.) This is one form of far-sightedness, known as *hypermetropia*.[3] Similar conditions are caused by anomalies in the refracting media of the eye.

---

[1] From ἔμμετρος, proportional, and ὤψ, ὠπός, eye.

[2] From μυώψ, μυῶπος, short-sighted.

[3] From ὑπέρμετρος, out of proportion, and ὤψ, ὠπός, eye.

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Females usually have slightly smaller eyes than males, as is shown by the table; yet this is by no means universal. When in popular language the size of the eyes is mentioned, it is usually their prominence that is noted rather than the actual dimensions of the organs, as the position of the eyes in the orbits causes a change in their apparent size according as they retreat or are set forward.

The axial length of the eyeball at birth is stated by Jäger to be 17.53 millimetres. The diameters are then approximately equal, the spherical form being more nearly realized, and the child is usually hypermetropic. Increase in size is slow during the first year, after that pretty regular up to puberty, when full dimensions are attained. The cornea grows faster proportionally, attaining its adult dimensions about the third year.

Comparing the eyes of different animals, it is found that their size does not depend upon the gross bulk of the animal, but rather upon the necessity which it has for acute and instant vision. In proportion as the globe of the eye is larger the refracting media (cornea and lens) are farther distant from the retina, the image produced is larger, and its details are more readily and quickly made out. Hence we find that animals requiring to move quickly have larger eyes in proportion to the size of the body,—the eye of an antelope, for example, being larger than that of an elephant. The eye of the chimney-swallow is one-thirtieth the volume of the body, while the viper's eye is but one-thousandth. The eyes of all birds are relatively larger than those of mammals.

In animals of the same general habits the smaller ones have the larger eyes. The wild cat, for example, has larger eyes proportionally than the lynx, and the lynx larger than the lion.[1] Nocturnal animals usually have large eyes, and this is also the case with many fishes. It has been suggested that the larger size of the retinal image in these animals compensates to some extent for the small amount of light to which they are accustomed.

The average weight of the eyeball may be considered as about seven grammes.[2] At birth it weighs about 3.8 grammes, being much larger and heavier in comparison with the entire body than is the eye of the adult.

The weight of the two eyes as compared with the rest of the body is at birth as 1 : 419, while at adult age it is but as 1 : 4832. While the body increases in volume 21-fold from birth to adult age, the eye grows about 1.8-fold.[3] Like the brain and the ear, the eye attains its structure and

[1] See on this subject Emmert and Fischer, in Corresp.-Blatt f. Schweiz. Aerzte, 1887, p. 275. Also Nuel, in Dict. encycl. des sciences médicales, article Œil.

[2] This is the average given by Merkel (Gräfe and Sämisch's Handbuch der gesammten Augenheilkunde) and Schäfer (Quain's Anatomy, 10th edition). Other authorities state the weight as follows: Krause, 104 to 128 grains (6.74 to 8.79 grammes); Henle, 6.3 to 8 grammes; Huschke, 6.6 to 8.2 grammes; Sappey, Debierre, and Gerlach, 7 to 8 grammes; Testut, 7 to 7.5 grammes; Macalister, 7.2 grammes. It seems probable that in this, as in the measurements, allowance has not always been made for the rapidity of evaporation of the fluids of the eye after death.

[3] Vierordt, Daten und Tabellen.

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proportions much earlier than the rest of the body, an arrangement which seems to be required by the needs of the organism. Its volume is about 6.5 cubic centimetres,[1] and its specific gravity must therefore be about 1.077.[2]

RELATIONS.

The eye is situated in the bony cavity of the orbit, in which it is held by appropriate fascia; about one-third of its anterior surface is free, or, to be more exact, covered only by a thin transparent pellicle derived from the epidermis, called the conjunctiva, and protected by movable curtains of integument, the eyelids; the posterior two-thirds are separated from the orbital fat by an aponeurosis called the bulbar fascia, within which the eye rolls like a ball within a socket, its attachments being so slight that when the conjunctiva is severed and the attached muscles, vessels, and nerves are cut, the globe may be removed like a nut from its shell. We have then to consider the relations of the eyeball to (1) the orbit, (2) the eyelids, (3) the conjunctiva, and (4) the bulbar fascia.

Shaped like an irregular, prostrate cone or pyramid with rounded angles, the orbit is longer on the temporal side and on the floor than on the nasal side and roof; its apex is situated at or a little below the optic foramen, and its base at the facial surface is bounded by the edges of the orbital arches.

Its average dimensions have been carefully calculated by Emmert[3] from a series of selected skulls free from abnormalities, as follows:

	Adult Males, 20 to 67 Years.	Adult Females, 23 to 67 Years.	Children, 10 to 17 Years.
	Millimetres.	Millimetres.	Millimetres.
Width	41.6	39.8	34.3
Height	34	33.6	29.2
Depth	39.8	39.4	34.75
Length of external wall	46.4	46	39.4
Length of internal wall	41.4	40.3	36
Distance between outer edges of orbits	99.7	96	80.8
Distance between axes of orbits	60	58.3	48.1
Angle which facial openings of orbit make with each other	147°	146.5°	144.6°
Angle between orbital axes	43 4°	44.7°	42.4°
Angle between external orbital walls	89.9°	89.9°	87.4°

The dimensions of the orbit have some ethnological importance. In

[1] This is the estimation given by Schäfer. Henle gives it as 6 cubic centimetres; Vierordt, 6.6 cubic centimetres; Macalister, a little over 6 cubic centimetres.

[2] The following statements concerning the specific gravity of the eyeball may be cited: Huschke (Bau des menschlichen Körpers, vol. v.), 1.022 to 1.0302; Fricke (cited by Vierordt in Daten und Tabellen für Mediciner), 1.212 to 1.0302; Davy (Transactions of the Med.-Chir. Soc. of Edinburgh, vol. iii.), 1.091; Macalister (Text-Book of Human Anatomy), 1.025. The latter author seems to have overlooked the fact that when the weight and volume of a body are given the specific gravity can be deduced. From his figures of weight and volume the specific gravity would be more than 1.100.

[3] Emmert (Emil), Auge und Schädel, Berlin, 1880. These measurements are, on the whole, the most extensive, and very carefully taken. Authors vary as to the dimensions

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anthropoid apes the height is greater than the breadth. In man at birth the two are nearly or quite equal, and this primitive condition is retained among the Polynesians and the Chinese, also to some extent in females of the Indo-European races, who generally have orbits higher in proportion to their width than males have. Some savage races, however, such as the Kaffirs and the Tasmanians, have orbits very low in proportion to their width.

The axes of the two orbits are not parallel, but, as stated above, are inclined at an angle of from 42° to 45°,[1] and are depressed below the horizontal plane from 15° to 20°. The ocular and orbital axes cannot, therefore, coincide. The average distance between the anterior poles of the ocular axis is from fifty-eight to sixty millimetres. (Merkel.)

The eye is so situated in the orbital cavity that a line drawn from the upper to the lower orbital margin just touches the cornea (Fig. 8); the back part of the ball is therefore from sixteen to eighteen millimetres from the optic foramen. It is not exactly in the axis of the cavity, being one or two millimetres nearer to the temporal side than to the nasal, and a little nearer to the upper than to the lower orbital margin. (Fig. 9.) A section through the orbit farther back (Fig. 10) shows that at the equator it lies at about the same distance from the upper as from the lower wall.

The capacity of the adult orbit is about thirty (twenty-five to thirty-

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of the orbit, as will be seen from the following table. This is mainly due to different methods of measurement.

	Breadth.	Height.	Axial Length.
	Millimetres.	Millimetres.	Millimetres.
Merkel (Topographische Anatomie)	♂ 40.5 ♀ 40	35 34.5	43 40.5
Arlt (Archiv für Ophthalmologie, 1857)	36	30	42
Richet (Anatomie chirurgicale)	40–46	40	45–50
Luschka (Anatomie des Menschen)	50	40	. .
Vierordt (Daten und Tabellen)	36	33	47
Benedikt (Eulenberg's Real-Encyclopädie)	39	♂ 33 ♀ 34	. .
Gerlach (Specielle Anatomie des Menschen)	42	35	43
Gayat (Annales d'oculistique, 1873)	42	36	. .
De Wecker (Traité des maladies des yeux)	39	35	. .
Tillaux (Anatomie topographique)	40	35	40–50

Broca (Topinard's Anthropologie) found that in different races of men the following were the average distances from the optic foramen to the superior border of the orbit:

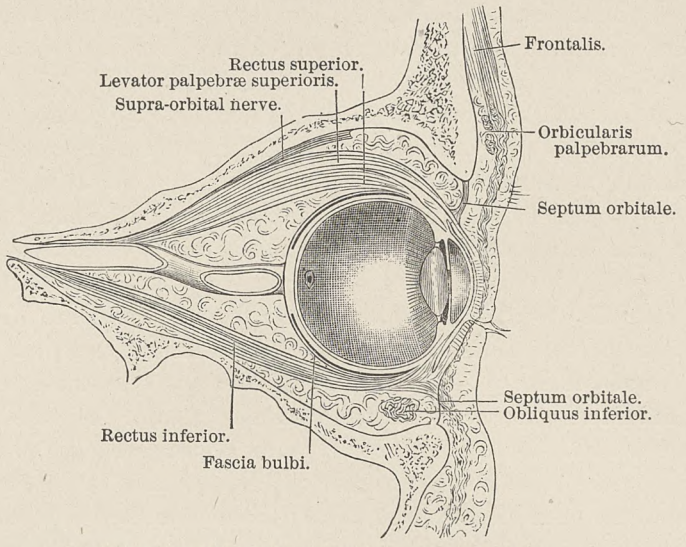
	Millimetres.		Millimetres.
Esquimaux	57.7	Spanish Basques	47
Usbecks	57.5	French Basques	50.2
Australians	56.2	Dutch	49.8
Chinese	55.6	Arabs	50.3
New Caledonians	55.6	Parisians, twelfth century	49.6
Papuans	55.8	Contemporary Parisians	50.9

[1] 46°. (Testut.)

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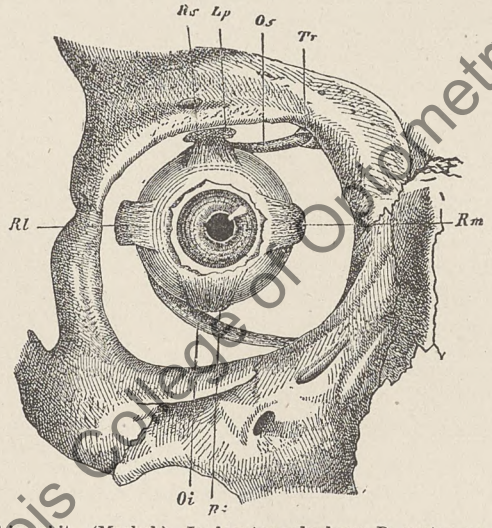
three) cubic centimetres, according to Gayat,[1] that of a child of ten years being twenty-two cubic centimetres. The eyeball, therefore, occupies about one-fifth of the cavity.

FIG. 8.



Sagittal section of the orbit and eyeball. (After Merkel.)

FIG. 9.



Position of eyeball in orbit. (Merkel.)—*Lp*, levator palpebræ; *Rs*, rectus superior; *Rm*, rectus medialis; *Ri*, rectus inferior; *Rl*, rectus lateralis; *Os*, obliquus superior; *Tr*, its trochlea *Oi*, obliquus inferior.

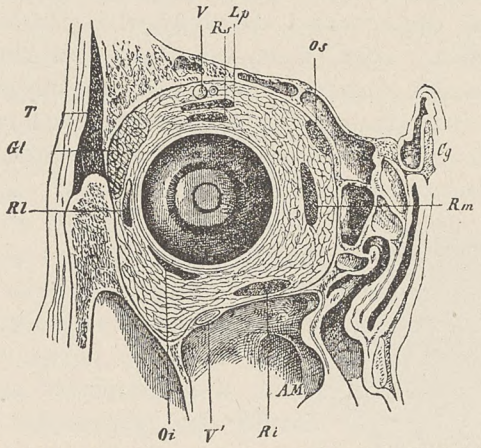
Where can the eyeball best be reached for examination or operation? It is obvious that above it is quite well protected by the overhanging edge

[1] Gayat (J.). Essais de mensuration de l'orbite. Annales d'oculistique, Bruxelles, 1873, lxx. 5–20.

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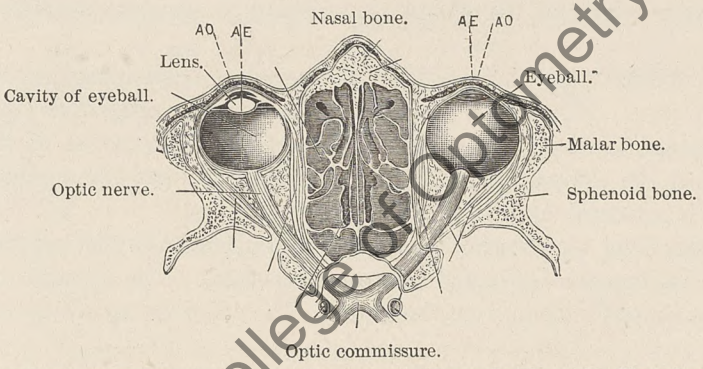
of the orbit and the superciliary arch. On the inner side also it is not easily accessible, owing to the projection of the bridge of the nose. Below, the orbital rim is smooth and projects but little, so that the depths of the orbit are readily reached. But the eyeball itself is more readily accessible on

FIG. 10.



Frontal section of the orbit and eyeball just anterior to the equator. (Merkel.)—*Am*, maxillary sinus; *Cg*, crista galli; *Gl*, lacrymal gland; *Lp*, levator palpebræ; *Oi*, obliquus inferior; *Os*, obliquus superior; *Ri*, rectus inferior; *Rl*, rectus lateralis; *Rm*, rectus medialis; *Rs*, rectus superior; *T*, temporal muscle; *V*, *V'*, veins.

FIG. 11.



The eyes and optic nerves seen from above after removal of the roof of the orbit.—The left eye is shown in section. *AO*, axis of orbit; *AE*, axis of eye.

the outer side. If a line is drawn touching the orbital rim on either side it will cut the ball quite back of the cornea. (Fig. 11.) This is due partly to the direction of the orbital axis and partly to the fact that the rim retreats here to some extent.[1] By suitably moving the eye the ball can be

[1] It may be interesting to note that in most mammals the external wall of the orbit is but little developed. The malar bone does not send a process up to the frontal, and the orbit communicates widely with the temporal fossa.

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explored here almost as far back as the equator, while above and below only a small strip of the sclera can be felt.

In considering the relations just described it should, however, be remembered that the situation of the eyeball in the orbit is subject to considerable variations, both physiological and pathological. A greater or less amount of orbital fat may shove it forward, producing a staring expression, or cause it to sink deeper within the cavity, as in the hollow-eyed aspect of severe emaciation. Cohn[1] found variations of as much as ten millimetres behind the edge of the orbit and twelve millimetres in front of the same in healthy individuals. The forward projection may indeed reach twenty-four millimetres in unusual cases. The condition of protrusion is known as *exophthalmos*,[2] the reverse as *enophthalmos*.[3] Protrusion may be produced also by various other causes, such as paralysis of the recti muscles (also seen when their tendons are cut) or the distention of the intra-orbital vessels. The sudden staring during surprise or terror is probably due to the latter cause, as is also the protrusion seen in some females during menstruation. Enophthalmos may arise from the sudden draining of fluid from the tissues in Asiatic cholera, from atrophy of any of the orbital contents, from any injury or disorder that enlarges the orbital cavity, or from paralysis of the sympathetic nerve. In the latter case it has been suggested that the disturbance is caused by the effect of this paralysis upon the orbital muscle of Müller,[4] a thin sheet of non-striated muscular fibre that lies in the membrane that stretches over the spheno-maxillary fissure. Losing its tonicity by a paralysis of its nerve-supply,—the sympathetic,—it permits a bulging of the orbital contents and consequent retraction of the eyeball.

The eyelids[5] vary their relation to the eyeball according as they are closed or open. When open (Fig. 12) they form a considerable aperture, the *palpebral opening*,[6] curved above and below by the edges of the two lids, which are united internally and externally to form the angles of the eye.[7] The external angle of the eye is said by Testut to be ten to twelve millimetres from the cornea, five to six millimetres from the orbital arch, and ten millimetres below the fronto-malar suture. The internal angle is five to seven millimetres from the globe. The opening exposes nearly one-

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[1] Klinische Monatsblatt, 1867.

[2] From ἐξόφθαλμος, having prominent eyes.

[3] From ἐν, within, + ὀφθαλμός, eye: having eyes deeply set.

[4] Named in honor of H. Müller, an ophthalmologist of Würzburg, born 1820, died 1864.

[5] Syn.: *palpebræ*.

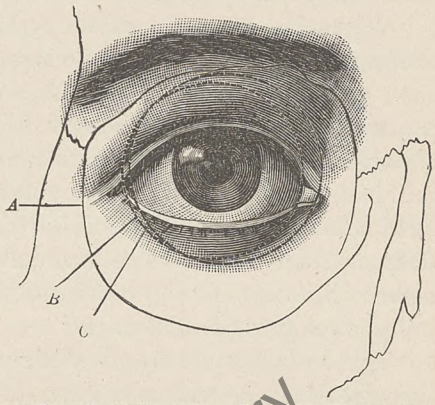
[6] Syn.: *rima palpebrarum*, the palpebral slit, is used to indicate the slit between the eyelids, whether closed or open. *Fissura palpebrarum*, the palpebral fissure, may be used in the same sense. *Rictus palpebrarum*, or gape of the eyelids, is used to indicate the space between the open lids.

[7] Syn.: corners of the eye; palpebral commissures; *anguli oculi*, or *canthi oculi*, or *commissuræ palpebrales externæ* and *internæ*, or *laterales* and *mediales*, or *temporales* and *nasales*, or *minores* and *majores*.

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fifth of the surface of the ball,—nearly the whole of the cornea and a considerable portion of the sclera. Its longitudinal axis is not quite horizontal, the outer angle being ordinarily slightly inclined upward and situated about four millimetres above a horizontal line. This inclination is greater in the Mongolian and other Altaic or Mongoloid races, as the Samoyedes, Finns, and Esquimaux. Mondière[1] found that an average of three hundred measurements of these peoples gave an upwardly sloping angle of nearly five degrees. The palpebral opening is somewhat less than thirty millimetres in length (including five to seven millimetres for the little recess at the inner angle known as the lacrymal bay[2]), being less in females. It is curved more above than below, and when this curvature is excessive, as it sometimes is in persons with prominent eyes, the "almond eye" so much praised by Eastern poets is produced. It may be noted that the height of the opening is usually somewhat less among Orientals than with Europeans. While subject to a considerable degree of variation, the opening may be stated as being from twelve to fifteen millimetres high when opened widely without raising the eyebrows or wrinkling the skin of the forehead. In children the length of the palpebral fissure is unusually great, and this, in conjunction with the greater elasticity of the skin of the lids, is the cause of their widely opened eyes. There appears to be a slight decrease in the length of the fissure in old age.[3]

FIG. 12.



The palpebral opening. (Merkel.)—The contour of the underlying bones is shown by the unbroken line, *A*; that of the eyeball by the broken line of short spaces, *B*; that of the conjunctival sac by the broken line of long spaces, *C*.

With eyes looking straight ahead, the edge of the lower lid touches the bottom of the cornea or falls slightly below it, and the upper lid usually impinges upon the cornea about one or two millimetres. When looking upward, the upper lid rises and the palpebral opening dilates so that a strip of the sclera is visible below. When looking downward, the upper lid sinks to the upper border of the pupil, the lower remaining at the central margin. When the eyes are fully closed, the upper lid descends to the lower edge of the cornea, the inner angle remains fixed by the palpebral ligament, but the outer angle descends about five millimetres. During sleep or unconsciousness the eyes turn slightly upward and inward.

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[1] Mémoires de la Société d'Anthropologie, 1875, ii. 451.

[2] Syn.: *lacus lacrymalis*.

[3] Fuchs (Ernst). Zur Physiologie und Pathologie des Lidschlusses. Archiv für Ophthalmologie, xxxi., 1885, Abth. II. 97.

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The *conjunctiva*[1] is a layer of mucous membrane of a lymphoid character, continuous with the epidermis at the edges of the lids, lining their deeper surfaces (palpebral conjunctiva[2]), being thence reflected upon the eyeball (ocular conjunctiva[3]), and entirely covering its anterior third. The place of reflection is called the *fornix*[4] of the conjunctiva. It will be seen that when, by closing the lids, the edges of the palpebral conjunctiva are brought together, the entire membrane forms a closed sac,—the conjunctival sac,[5]—applied to the front of the eye, reminding one of the arrangement of the lining of the serous cavities of the body. When the lids are parted this sac is opened, and any small foreign bodies that impinge against the anterior surface of the eye are likely to lodge in it. Its extent and relations to the surrounding structures should, therefore, be noted.

When the eyes are open the fornix is about thirteen millimetres from the edge of the upper lid, while it is but nine millimetres from the lower lid. On the sides also the sac varies in depth, forming at the lateral angle a shallow pocket five millimetres deep, but at the medial angle becoming almost obliterated by the semilunar fold, under which it passes for only two millimetres. The fornix is five millimetres from the orbital rim above, six millimetres below, and four millimetres at the lateral angle. (Gerlach.) Its distance from the cornea is stated by Testut to be ten millimetres above, eight millimetres below, fourteen millimetres at the lateral angle, and seven millimetres at the medial angle.[6]

The ocular conjunctiva is distinguished from the palpebral by its less vascular condition and paler tint. It is divided into a scleral[7] portion and a corneal portion,[8] which differ somewhat in structure, the scleral being composed of stratified pavement epithelium with a regular submucosa, while the corneal has an epithelial layer only, the submucous tissue blending with the corneal tissue proper, or being reduced to a very delicate structureless layer. Near the cornea it is closely adherent to the sclera, often in adults forming a slightly thickened ring containing numerous vascular papillæ and known as the *limbus conjunctivæ*.[9] Fatty deposits[10] are frequently seen on the medial side of the limbus, especially in old age.

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[1] From L. *conjunctivus*, *-a*, *-um*, serving to connect, because it connects the eyelids with the ball. Syn.: *membrana conjunctiva*; *Bindehaut*, G.

A more complete description of this membrane is given, under the anatomy of the appendages of the eye, on pp. 89, 90.

[2] Syn.: tarsal conjunctiva; *conjunctiva palpebrarum.*

[3] Syn.: *conjunctiva oculi* or *bulbi.*

[4] From L. *fornix*, *fornicis*, an arch or vault. Gerlach improperly calls the conjunctival sac the fornix. Syn.: fold of transition; conjunctival cul-de-sac; *fornix conjunctivæ.*

[5] Syn.: *saccus* or *sinus conjunctivæ.*

[6] Merkel gives the distance above as eight millimetres; below, ten millimetres. It doubtless varies considerably with the prominence of the eyes.

[7] Syn.: *conjunctiva sclerotica* or *bulbi*; *tunica adnata oculi.*

[8] Syn.: *conjunctiva corneæ.*

[9] Syn.: *annulus conjunctivæ*; *limbus corneæ.*

[10] Pinguecula.

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The external part of the scleral conjunctiva is united to the ball by connective tissue partly condensed, a continuation of the bulbar fascia, and in part quite lax, continuous with the adipose capsule of the eye. The laxity of the union of the conjunctiva with its subjacent tissues, both at the fornix and upon the sclera, secures the necessary freedom of movement to the ball. In whatever direction the eye may be moved, the conjunctiva on the opposite side is stretched. At the nasal side, where the fornix lies so near the ball, movement is provided for by an accessory fold (the semilunar fold[1]), a vestige of the third eyelid found in some lower animals. The laxity of the tissues beneath the conjunctiva makes it very easy to raise it whenever it is necessary to perform any operations within the orbit. It also explains the frequency of ecchymosis in this situation. Sometimes, indeed, a fracture of the base of the skull or other internal injury causing the rupture of vessels may become known by an ecchymosis of the scleral conjunctiva, the blood gradually infiltrating the looser tissues of the orbit and appearing at last upon the ball. If desirable to fix the eyeball for the performance of any operation, the conjunctiva should be seized near the cornea, where it is more firmly attached.

The part of the orbit not occupied by the eyeball is filled with loose connective tissue enclosing in its meshes masses of fat, and therefore often called the *adipose body* of the orbit.[2] This fills in all the interstices between the muscles, nerves, and vessels that pass forward to the ball, making an excellent padding, in which all these structures can lie without being disturbed by shocks or displaced by the ocular movements. About the ball this connective tissue is condensed to a firm aponeurosis that effectually confines the loose tissue, leaving the eye comparatively free.

The researches of Schwalbe[3] have demonstrated that this *bulbar fascia*, or *capsule of Tenon*,[4] is in reality the lining membrane of a lymph-lacuna, the *interfascial space*,[5] that surrounds the ball, and communicates on the one hand with the intra-ocular space between the chorioid and the sclera (perichorioideal space), and on the other with the perineural space about the optic nerve, and thence through the interstices of the dural sheath with the subdural and subarachnoid spaces of the cerebral meninges. (See Fig. 13.)

The bulbar fascia passes forward and is attached to the deeper surface of the conjunctiva near the edge of the cornea, and is there reflected upon the sclera, adhering closely to it and clothing the posterior two-thirds of the surface of the globe with an extremely delicate layer.

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[1] Syn.: semilunar plica; nictitating membrane; *plica semilunaris; palpebra tertia; membrana nictitans.*

[2] Syn.: *corpus adiposum orbitæ; capsula adiposa bulbi;* adipose capsule of the eye.

[3] Archiv für mikroskop. Anat., vi. 41, 1870.

[4] Named for Jacques-Réné Tenon, a surgeon of Paris, born 1724, died 1816.

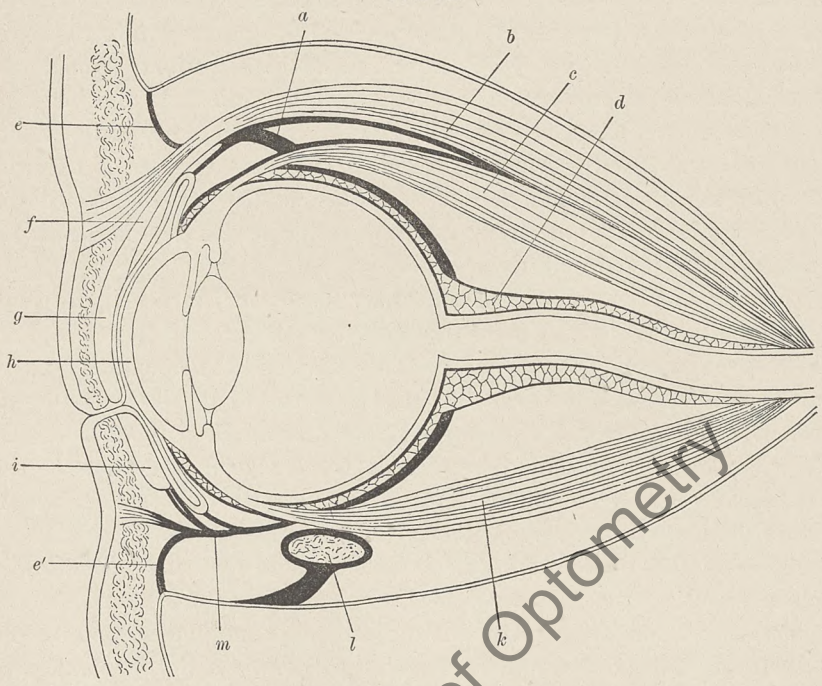
Syn.: *aponeurosis orbito-ocularis* (Richet); orbital aponeurosis; orbito-ocular aponeurosis or fascia; *fascia bulbi* or *Tenoni; tunica vaginalis oculi* (Hyrtl) or *bulbi;* vaginal tunic (Leidy); *capsula fibrosa bulbi;* Bonnet's capsule.

[5] Tenon's space (Schwalbe); supra-scleral space; *spatium interfasciale.*

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Like a serous membrane, the fascia has, therefore, a parietal layer against the orbital fat, constituting the capsule of Tenon in the more restricted and usual sense, and a visceral layer ensheathing the eyeball, and sometimes called the *episclera*. These layers are not, however, totally separated from each other, as are those of a serous membrane, but are united by fine trabeculæ[1] that cross the periscleral space and are sufficiently lax to allow the eye to move with perfect freedom. The entire internal surface of the capsule, together with the trabeculæ, is lined with endothelium. It is, there-

FIG. 13.



Sagittal section of the eye, showing the bulbar fascia and its attachments.—*a*, prolongation of bulbar fascia; *b*, levator palpebræ; *c*, rectus superior; *d*, perineural space; *e*, *e′*, septum orbitale; *f*, tendon of levator; *g*, tarsus superior; *h*, cornea; *i*, tarsus inferior; *k*, inferior rectus muscle; *l*, inferior oblique muscle; *m*, prolongation of bulbar fascia.

fore, anatomically similar to the lymph-sacs found elsewhere in the body, as the subarachnoidal sacs, and the perivascular sheaths of the vessels of the pia mater and of the mesentery.

The structures attached to the eyeball pass through this fascia and receive investments from it. Behind, about the optic nerve, it becomes looser in texture, and permits the passage of fluid between that nerve and the ciliary vessels and nerves, along an area one centimetre in diameter.

The interfascial space contains a small amount of fluid derived from the vessels that supply its walls, and in this, as in other respects, shows considerable analogy to the synovial cavity of an arthrodial joint.

[1] *Adventitia oculi.* (Lockwood.)

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THE EXTERNAL OR FIBROUS COAT.[1]

The essential characteristics of this envelope depend upon its structure, which is of firmly condensed fibrous tissue. Hence it is strong, comparatively inextensible, and has a capsular character resembling in some respects the tunica albuginea of the testis. It is much the thickest of the three coats, and serves as a protecting envelope to the inner, more delicate structures, its office being like that of the dura mater of the central nervous system, with which, indeed, it is continuous through the fibrous sheath of the optic nerve. In view of this special character, it is not strange that in lower vertebrates portions of this capsule become cartilaginous, or even ossified. In fishes and amphibia it becomes cartilaginous only, while in reptiles and birds it is cartilaginous behind and often protected in front by a ring of platelets of bone called sclerotals. In mammals it is, however, almost invariably fibrous, the only exception being the lowly monotremes, which in this as in so many other particulars show their affinity with birds and reptiles. In most mammals the eye is efficiently protected by the walls of the orbit, and it is perhaps for this reason that no ossification of the capsule occurs. Calcareous deposits are sometimes found in the external coat, but the normal interstitial tissue never ossifies, this occurring only in exudations from the chorioid arising under pathological conditions.[2]

Unlike the other coats, which are incomplete at some part of the circumference, the fibrous coat forms a complete investment, with the exception of such orifices as are necessary for the passage of the vessels and nerves that supply the interior.

The normal tension of the capsule is said to be equal to that produced by a column of mercury twenty-six millimetres high, and is quite sufficient to make the ball firm and resistant to the touch. Under pathological conditions it may vary considerably, reaching as high as seventy millimetres of mercury. When unusual pressure is induced by inflammatory processes, such as engorgement of vessels, effusions, etc., it reacts upon the contents of the eyeball because of the unyielding and inextensible character of the external coat, injuring and finally destroying them. This character appears to be less marked in childhood than in later years, possibly because the coat is then thinner: hence a very considerable expansion of the ball may occur in hydrophthalmos. It may also occur in the adult when the tissues are softened by inflammation, but this is due to degenerative changes rather than to a true elasticity.

Like most structures of condensed connective tissue, the capsule is scantily supplied with blood-vessels and has no proper lymphatics, the place of the latter being supplied by lymph-lacunæ.

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[1] Syn.: *tunica externa* or *fibrosa*; *capsula fibrosa* (H. Meyer); *dura oculi*; *pachymeninx ophthalmencephali*. The two latter terms relate to the conception that the external coat is an extension of the dura mater of the brain.

[2] Grossmann (L.). De l'ossification dans l'œil. Arch. d'ophth., Paris, 1889, ix. 137.

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THE SCLERA.

The *sclera*,[1] or posterior portion of the capsule, is white and opaque. It is, as Bowman has pointed out, an excellent example of change produced in the optical properties and appearance of a substance by structural peculiarities. Although it has essentially the same fibrous constitution as the transparent cornea, yet, as its fibres are arranged irregularly, some running in a meridional direction and others equatorially, and by no means lying in concentric lamellæ, it almost wholly intercepts the transmission of light. It has not even the silvery sheen of aponeurotic tissues caused by the parallel but wavy course of contiguous fibres, but is a dead white, owing to the dispersion of the rays by its felt-like web, the glistening reflection that occurs from its anterior exposed portion being due rather to the moist conjunctiva than to the properties of the cornea itself.

While the tissue is mainly of the white, fibrous variety, there is yet a considerable number of yellow, elastic fibres scattered through it, especially at the anterior part of the globe and at the canals for the passage of vessels and nerves. On the inner surface these elastic fibres become more numerous and connect with the elastic net-work of the chorioid. Like the fibres of that membrane, they have among them a considerable number of pigmented cells, so that when the sclera is separated from the underlying coat, which is easily done because of an intervening lymph-space, its concave surface is seen to be brownish fading to a dirty white in front. It is therefore known as the *lamina fusca*[2] (Brücke), although it is by no means a separate sheet, but rather an intrusion, more or less extensive, of the peculiar pigment of the chorioid into the deeper portion of the sclera. (See Fig. 14.) This pigment, together with that of the darker chorioid, may sometimes show faintly through the sclera, imparting to it a bluish tint like that of skimmed milk or of some kinds of porcelain. This is usual in children, in whom the sclera is thin, and may also be observed in dark races and in brunettes of the white race, in whom the pigment is more copious. It is not infrequently seen during congestion of the internal coats of the eye. The pigmented cells are sometimes scattered in irregular masses throughout the entire substance of the cornea, even on its outer surface, especially near the exits of the anterior ciliary veins. This is quite common among negroes. In old age the sclera becomes of a dull yellowish hue, due to the infiltration of fat. This is especially marked in the neighborhood of the cornea. If abrasions of the conjunctiva exist, the sclera may be darkened by the incautious use of eye-washes containing nitrate of silver.

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[1] From *σκλήρος*, hard. Syn: *tunica sclerotica; sclerotica;* sclerotic coat; sclerotic; *tunica alba* or *albuginea;* white of the eye; *cornea opaca.*

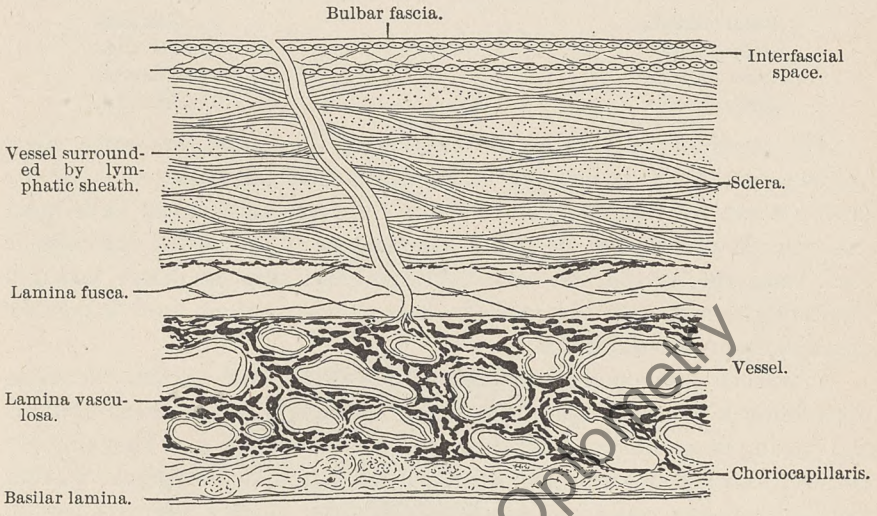
According to Hyrtl (Onomatologia anatomica), sclera is the older term and more accurate etymologically. Oribasius calls the outer coat *σκληρά μῆνιγξ* (*dura membrana*), and Galen *παχὺ καὶ σκληρὸν σκέπασμα ὀφθαλμοῦ* (*crassum et durum involucrum oculi*). Sclerotica is a barbarism that first appears in the Latin translations of Rhazes and Avicenna.

[2] From L. *fuscus*, *-a*, *-um*, dark, dusky, swarthy. Syn.: *tunica arachnoidea oculi.*

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The statement of Schäfer in the last edition of Quain's Anatomy, that the maintenance of the form of the eye chiefly depends on the sclera, is inexact. In some of the lower vertebrates, it is true, the sclera is rigid and maintains its form after the contents of the globe have been evacuated, but in man it is the pressure of those contents that controls the form; when they are copious the globe is full and round, when scanty it is flaccid or collapsed. Behind, where the sclera supports the retina, and where constancy of curvature is important in order that the optical image may be accurately projected, the greatest thickness is found, reaching nearly one millimetre in the neighborhood of the optic nerve. From this region forward it grows rapidly thinner until, just behind the insertion of the recti muscles, its thickness is no more than four-tenths of a millimetre. Here

FIG. 14.



Transverse section of sclera and choroid. (Altered from Testut.)

it is liable to bulge when intra-ocular pressure is increased, and here also perforation and evacuation of pus occur when deep-seated inflammations are neglected. In front of the insertion of the tendons it receives a reinforcement due to a blending with their tissue, being six-tenths of a millimetre thick. Yet this appears to be the weakest part of the capsule, for it is here, near the corneal margin, that the eye usually ruptures from external violence. Because of the inextensible character of the fibrous capsule, a rupture is almost invariably by *contre-coup*,—that is to say, opposite the side on which the blow is received.

An idea of the density of the scleral tissue may be obtained by comparing its weight with that of the entire eye. The most recent estimates on this subject are those of Testut, who found that an average taken from both eyes of five adults showed that the sclera is about one-sixth the total

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weight of the eye.[1] Among previous observers, Sappey states it as one-ninth, while Huschke gives it as one-fourth, which seems unreasonably large.

The external surface of the sclera is, as has already been mentioned, clothed with episcleral tissue connected with the orbital aponeurosis. Anteriorly this is continuous with the subconjunctival connective tissue. Within this tissue there runs a net-work of vessels connecting with those of the conjunctiva, but closely attached to the ball and not affected by the movements of that membrane. The injected appearance of this net-work may be an important sign in inflammation of the sclera.

The four recti muscles of the eye passing forward from the apex of the orbit are inserted by flattened tendons on the anterior portion of the external surface of the sclera, near the corneal margin. The distances from the cornea of the insertions of the several tendons can for practical purposes be remembered by the round numbers given by Tillaux, as follows:[2]

Rectus medialis	5 millimetres.
Rectus inferior	6 millimetres.
Rectus lateralis	7 millimetres.
Rectus superior	8 millimetres.

The proximity of the line of insertion to the cornea has some effect on the action of the muscle, for it is evident that the nearer it is set the farther it can roll the eye, and therefore the more effect it can have upon changing the direction of its axis. The tendons of the medial and inferior recti, being the nearest, can have a greater effect than the others, and it is interesting to note that it is precisely these muscles that are most frequently operated upon for strabismus.

It will be seen upon an inspection of Figs. 15 and 16 that the insertions follow a somewhat spiral course, commencing with the rectus medialis and passing downward and outward to the rectus superior. They are not, however, continuous with each other, and the idea sometimes advanced that there is a common sheet into which they all pass at their insertion has no foundation in fact.

The mid-points of the insertions of the rectus lateralis and medialis

[1] Accurately, as 1 : 6.15.

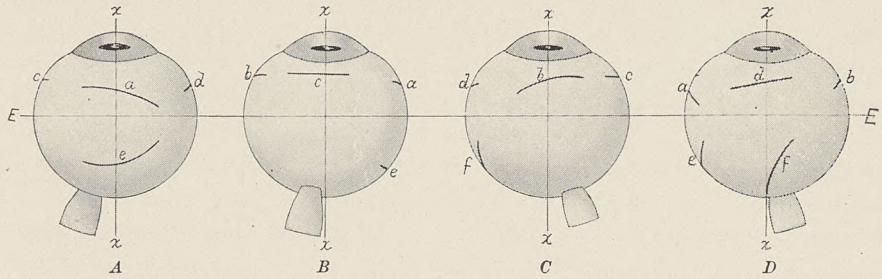
[2] The actual distances are given by different authorities as follows:

	Rectus Medialis.	Rectus Inferior.	Rectus Lateralis.	Rectus Superior.
	Millimetres.	Millimetres.	Millimetres.	Millimetres.
Fuchs	5.5	6.5	6.9	7.7
Testut	5.8	6.5	7.1	8
Gerlach	5.4	6.9	7.2	7.5
Sappey	5.5	6.7	7.2	8.5
Krause	6.91	7.07	7.85	7.54
Macalister	7	7	7.5	7.5

The measurements of Fuchs, being taken from a larger series of subjects, are perhaps most widely accepted. See also page 97. It should be noted that Merkel accepts Fuchs's measurements as more accurate than his own. See his Topographische Anatomie, i. 293.

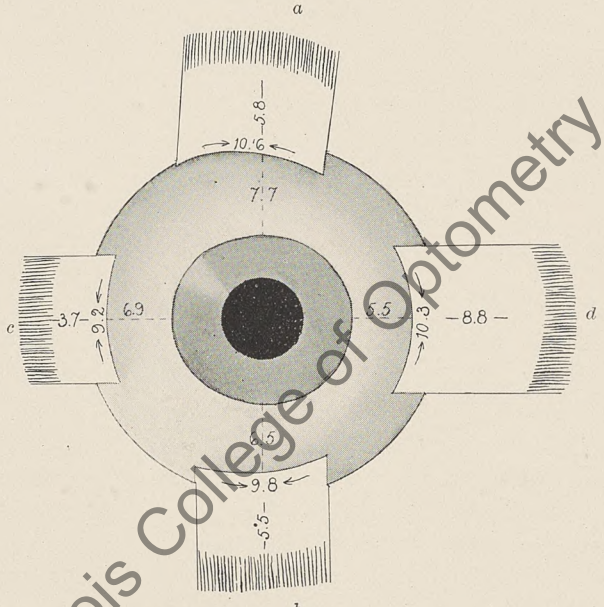
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FIG. 15.



Insertion of the ocular muscles upon the sclera of the right eye. (Drawn from the determinations of Fuchs.)—*A*, view from above; *B*, from nasal side; *C*, from below; *D*, from temporal side; *a*, rectus superior; *b*, rectus inferior; *c*, rectus medialis; *d*, rectus lateralis; *e*, obliquus superior; *f*, obliquus inferior; *EE*, equator; *xx*, axis.

FIG. 16.



Insertion of the ocular muscles upon the sclera of the left eye as seen from the front. (Drawn from the determinations of Fuchs.)—*a*, rectus superior; *b*, rectus inferior; *c*, rectus medialis; *d*, rectus lateralis.

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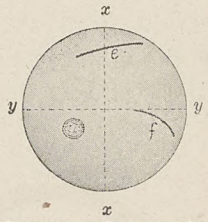
fall almost exactly in the horizontal meridian, while those of the rectus superior and inferior deviate somewhat from the vertical meridian, that of the latter muscle lying over one millimetre to the nasal side. (Gerlach.)

The lines of insertion are usually slightly curved, with the convexity towards the cornea. The ends of the lines of the rectus superior are sometimes bent abruptly backward. Occasionally the lines are not regularly curved, but wavy in their course.

The insertion is by no means a merely superficial one. The fibres of the tendon interpenetrate and firmly unite with the connective-tissue network of the sclera, spreading out in a fan-like manner, and thereby causing the thickening already referred to.

The oblique muscles are inserted well back in the posterior hemisphere of the eyeball, from six to eight millimetres from each other. (See Fig. 17.) The lines of their insertion are directed diagonally across the meridians, that of the superior oblique making an angle of forty-five degrees with the vertical meridian, while that of the inferior oblique makes with the horizontal meridian one of about nineteen degrees. Their insertions are not, therefore, parallel, as is sometimes stated. That of the superior oblique is mainly in the superior external quadrant of the hemisphere; its distance from the sheath of the optic nerve is from seven to ten millimetres, and its anterior end lies in about the same meridian as the external end of the rectus superior, from one-half to eight millimetres from it (average, 4.6 millimetres), and about the same distance behind the equator as the latter is in front. A sheet of firm connective tissue often unites the two tendons.

FIG. 17.



Insertion of the ocular muscles upon the sclera of the right eye, as seen from the rear. (Drawn from the determinations of Fuchs.)—*xx*, vertical meridian; *yy*, horizontal meridian.

Fuchs[1] states that there are two types of insertion of the superior oblique: one where the line has an equatorial direction and crosses the equatorial diameter, another where it is more nearly meridional and entirely in the external quadrant. In the first type the line is long, with a strong forward concavity, in the second it is shorter and flatter, beginning farther forward. The first is usual in emmetropic and hypermetropic eyes, the second in myopic. The emmetropic form is probably the primitive one, the myopic being a modification induced in early life by straining the muscle for near vision, this causing it to shift its insertion to a more favorable position by the well-known process of inducing atrophy by tension on one side while new fibres develop on the other. It should be noted, however, that the second variety may be found in eyes with perfectly normal vision.

The length of the line of insertion of the superior oblique varies considerably, as might be supposed from the above. Fuchs found that in

[1] Fuchs (Ernst). Beiträge zur normalen Anatomie des Augapfels. Archiv für Ophthalmologie, 1884.

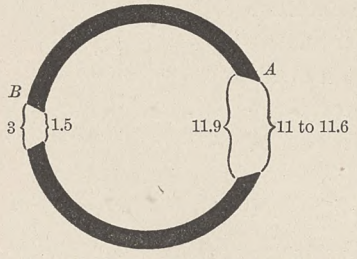
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thirty-one emmetropic eyes it averaged 10.7 millimetres (from 7.5 to 12.7), and that it was shorter in myopic eyes, in twenty of which it averaged 9.6 millimetres (from 6.8 to 14).

The inferior oblique is peculiar in having no tendon of insertion, its striated fibres passing close up to the sclera and even penetrating its substance. The line of insertion is very variable, as it usually lies in the inferior external quadrant of the posterior hemisphere and is affected by the antero-posterior extension that takes place in this region in myopic eyes. It is quite near the posterior pole, its distance from it averaging 2.2 millimetres in emmetropic and 4.1 millimetres in myopic eyes. The anterior end of the line is usually in the same meridian with the lower end of the insertion of the rectus lateralis, the two being about the same distance from the equator and about 9.5 millimetres (from 6.8 to 11.2 millimetres) apart. This separation is greater in myopic eyes. The insertion may lie partly or wholly above the horizontal meridian and be placed at varying degrees of obliquity. The line is usually a flat curve, with its convexity upward and a little forward. Further details are given on page 98.

Regarding the sclera as a segment of a spheroidal body, the surface appears incomplete in two places (Fig. 18): one in front, where the cornea is set, known as the *corneal interval;*[1] the other behind, where the optic nerve enters the *optic foramen* or *canal.*[2] At the corneo-scleral junction the irregular fibres of the sclera are intimately blended with the lamellated fibres of the cornea, and they are so arranged that the opaque sclera overlaps the transparent cornea externally, so that the edge of the foramen is bevelled at the expense of its interior surface. This bevelling is not uniform, being greater above and below than at the sides, so that the scleral limit appears anteriorly slightly elliptical with major axis horizontal, while within it is circular. The axes of the ellipse are 11 and 11.6 millimetres; the diameter of the circle is 11.9 millimetres. (Merkel.[3])

Fig. 18.



Intervals in the sclera. (Testut.)—*A*, corneal interval; *B*, optic foramen.

[1] Syn.: anterior scleral foramen; *foramen sclerœ anterius; foramen corneœ; rima cornealis.* (Anatomische Gesellschaft, 1895.)

[2] Syn.: *foramen opticum sclerœ* or *sclerotica.*

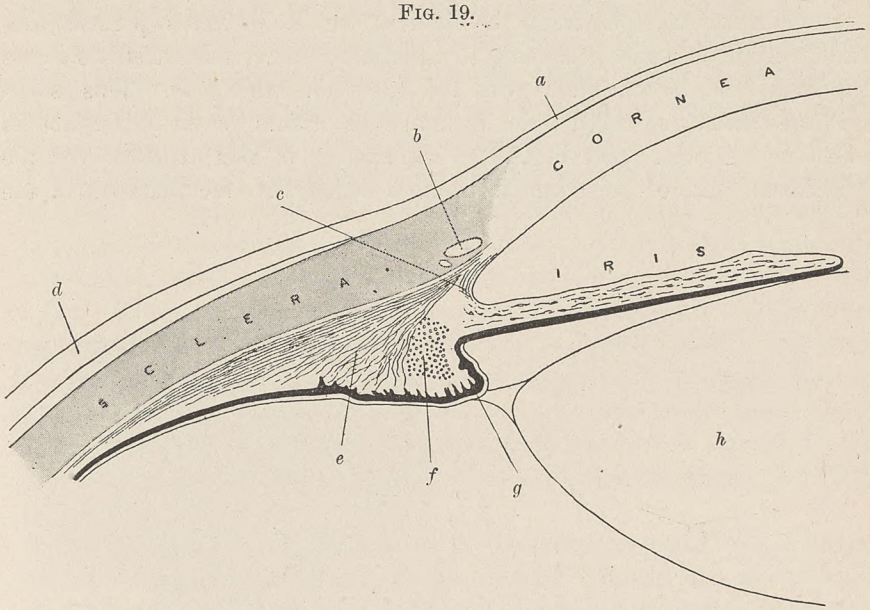
[3] The following measurements are given by other authorities:

	Ellipse.		Circle.
	Minor Axis.	Major Axis.	Diameter.
Schwalbe (following Helmholtz and Knapp)	11	11.9	..
Testut	11	12	13
Vierordt	..	..	12
Sappey	10	12	13

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Occasionally the innermost edge of the bevel overlaps the cornea slightly, thus making a regular setting or groove for it like the metal rim

FIG. 19.

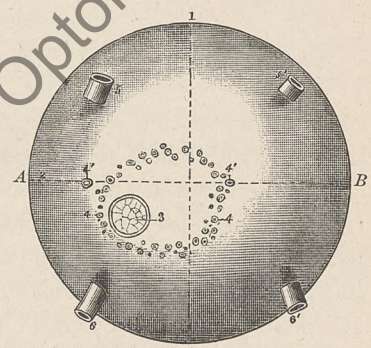


The junction of the sclera and the cornea.—*a*, corneal conjunctiva; *b*, scleral sinus; *c*, pectinate ligament; *d*, scleral conjunctiva; *e*, radial ciliary muscle; *f*, circular muscle; *g*, ciliary process; *h*, lens.

that holds a watch-crystal, and justifying the name of *Cornealfalz* (corneal groove or setting) that the German anatomists give to this junction.

The relations of the corneo-scleral junction to the structures within the eye should be carefully noted, as operative incisions are often made in this neighborhood. On examining Fig. 19 it will be seen that the iris is attached just at the posterior edge of the bevel, so that an incision at or even a little behind the anterior edge, which appears externally as the corneal margin, must necessarily enter the anterior chamber or space in front of the iris. To enter the posterior chamber or space between the iris and the lens, the incision or puncture must be from three to four millimetres behind the external corneal edge.

FIG. 20.



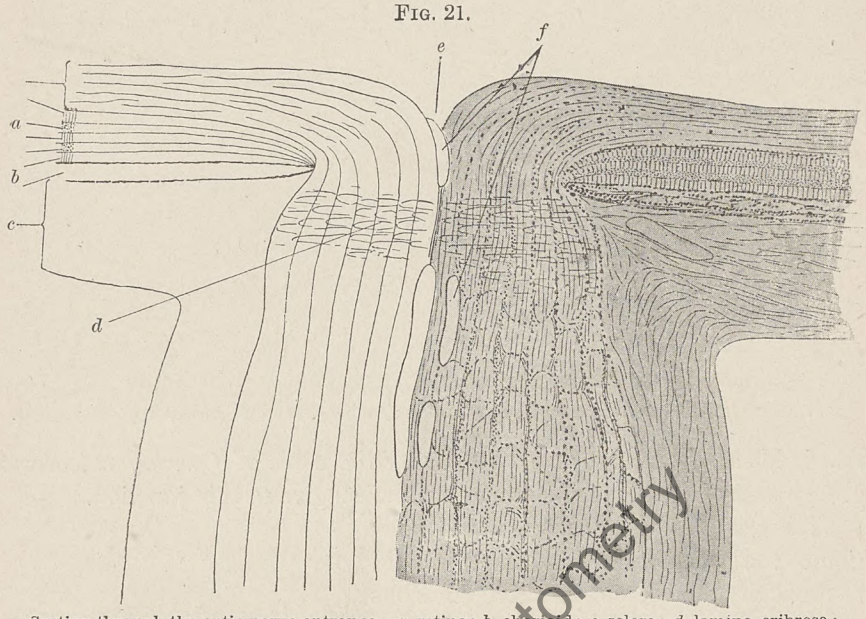
Posterior view of right eye, showing entrance of optic nerve. (Testut.)—*A*, nasal side; *B*, temporal side. 1, vertical meridian; 2, horizontal meridian; 3, optic nerve; 4, 4, ciliary vessels and nerves; 4′, 4′, long ciliary arteries; 5, 5′, superior vorticose veins; 6, 6′, inferior vorticose veins.

The optic foramen or canal of the sclera is situated about three millimetres from the posterior pole on the nasal side and about one millimetre below the horizontal meridian. (See Fig. 20.) By macerating a specimen it is easy to show that it is not a simple single

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canal, but a series of minute orifices through which pass the single fibres of the optic nerve. On reaching the sclera the external or dural sheath of the nerve becomes continuous with it, and the connective tissue that surrounds and interpenetrates the different bundles of fibres (perineurium, endoneurium) becomes condensed to a perforated sheet that stretches across the canal and is continuous with the sclera on either side. This is the cribrose lamina,[1] so called from its numerous orifices for the axis-cylinders of the nerve-fibres. (See Fig. 21.) The analogy of this structure with the cribriform plate of the ethmoid, through which pass the filaments of the

FIG. 21.



Section through the optic nerve entrance.—*a*, retina; *b*, choroid; *c*, sclera; *d*, lamina cribrosa; *e*, depression; *f*, blood-vessels.

olfactory nerve, and with the *tractus spiralis foraminosus* of the temporal bone, through which pass fibres of the auditory nerve, is very striking.

As the fibres of the optic nerve pass forward to go through the lamina cribrosa they lose their medullary sheaths. Hence the diameter of the nerve gradually decreases, and the optic canal of the sclera is funnel-shaped, its entrance being from 3 to 3.5 millimetres in diameter, its exit from 1 to 1.5 millimetres. All around the interior opening the sclera projects with a crest-like edge, which may be called the *pecten scleræ*,[2] or scleral rim. Hyrtl points out that the intimate connection between the sheath of the optic nerve and the sclera is the cause of the phenomena of subjective light sensations and weakness of vision which occur in rheumatic scleritis and other rheumatic inflammations of the eye.

[1] From L. *cribrosus*, *-a*, *-um*, riddled, perforated like a sieve. Syn.: *lamina cribrosa; cribrum.* (Langer.)

[2] From L. *pecten*, a comb or crest: the *Skeralkamm* of Gerlach.

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Besides these large openings in the sclera, there are other smaller ones, for the arteries, veins, and nerves that pass through it to supply structures in the interior of the eyeball. Of these there are three sets, situated respectively posteriorly, anteriorly, and midway between the other two.

The foramina of the posterior set are for the posterior ciliary arteries. These take a very oblique course through the sclera. Twigs from the short posterior ciliary arteries form a vascular circle around the optic nerve, known as the *circulus vasculosus nervi optici*, or *circlet of Zinn*.[1]

The foramina of the anterior set are for the anterior ciliary arteries and veins. Those for the veins are so small as to be barely visible, and are quite near the corneal edge; those for the arteries—five to eight in number—are larger, and are situated farther back, some two millimetres from the cornea. These vessels anastomose by episcleral branches with the conjunctival arteries, and then penetrate the sclera to supply the iris and other structures in the vicinity. Hence they are injected in iritis, and one of the most significant signs of that affection is a pericorneal blush about two millimetres from the corneal margin, from which it is separated by a grayish line corresponding to the scleral bevel, comparatively free from blood-vessels.

The foramina of the middle set are for the vorticose veins,[2] the principal venous channels of discharge from the eyeball. Fuchs has carefully investigated these important members of the circulatory apparatus of the eye. He finds their typical arrangement to be as follows. Four veins reach the ball, grouped in two pairs, an upper and a lower. The two veins of the upper pair lie on either side of the vertical meridian, but are not symmetrically placed with regard to it, the outer vein being somewhat the nearer to the meridian. They penetrate the sclera from 7 to 8 millimetres behind the equator, the external one being somewhat farther back than the other. The two veins of the lower pair have a similar relation to the lower half of the vertical meridian, but the veins penetrate the sclera somewhat farther forward, from 5.5 to 6 millimetres from the equator. All the veins pass through the sclera very obliquely, their courses trending forward and diverging from the vertical meridian. They emerge from the inner surface of the sclera from 2.5 to 3.5 millimetres behind the equator. Within the sclera each vein is surrounded by a perivascular lymph-space, across which pass fine trabeculæ of connective tissue that attach the vein to the wall of the canal. The other blood-vessels and nerves that pass through the sclera are also surrounded by lymph-spaces. All these open on one side into the perisclerał space, on the other into the perichorioideal space. Many variations of the vorticose veins occur. The number of the veins may be from five to seven, the internal ones being more frequently doubled

[1] Named for J. G. Zinn, a naturalist of Göttingen, born 1727, died 1759. Syn.: *circulus arteriosus nervi optici* or *Zinnii*; *Skleralgefässkranz*, G.; *Zinnscher* or *Hallerscher Kranz*, G.

[2] Syn.: *venæ vorticosæ* or *stellatæ*.

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than the others. When one of the veins divides before penetrating the sclera, its branches may pass for some distance along the surface before entering, reaching sometimes nearly to the insertions of the recti muscles.

Reference has been made (see page 104) to the effect which the oblique muscles of the eye have upon the vorticose veins. The veins on the outer side above and below may be compressed by the tendons of these muscles, those on the inner side being unaffected. The most favorable position for compression is that in which the eyes are adjusted for looking at near objects. Fuchs has suggested that this reduction of two of the principal venous exits of the eye may cause a stasis of blood with consequent increase of the internal pressure, which, when the eyes are young and the tissues flexible, may result in a lengthening of the antero-posterior axis, with consequent myopia. It is well known that children who are forced to use their eyes much in reading and other close occupations at an early age are likely to become near-sighted.

The internal surface of the sclera, bounded by the lamina fusca, is, like the external, separated from the neighboring tissues by a lymph-space, the perichorioideal space (Fig. 14), across which pass trabeculæ much thicker and stronger than those of the episclera. When the sclera is stripped away from the chorioid, its internal surface appears ragged and tattered because of the breaking and fraying of the trabeculæ that pass to the supra-chorioideal lamina of the chorioid, a tissue closely resembling the lamina fusca of the sclera. The pigmented character of the lamina fusca has already been mentioned. Like other lymphatic spaces, the perichorioideal space is lined with endothelium, which is continued upon the trabeculæ. It communicates with the periscleral space by means of perivascular and perineural lymph-channels, as before indicated. Along the walls of the perichorioideal space, making grooves in the lamina fusca, run the filaments of the ciliary nerves, which, having pierced the sclera near the posterior pole, are passing forward to be distributed to the cornea, the iris, and the ciliary muscle. Hence these nerves are confined between the chorioid and the inextensible sclera, and in case of any increase of intra-ocular tension they become compressed, often with serious consequences. In acute glaucoma —a disorder accompanied by increased pressure—the sensitiveness of the cornea and the reaction of the iris may be wholly abolished by compression of these nerves. The pain in these cases may be very severe and of a dull, sickening character like that in orchitis, which, it will be remembered, is also due to the compression of nerve-filaments against an inextensible fibrous envelope, the tunica albuginea testis. The long ciliary arteries also run along the walls of the space, and may be affected by compression.

In structure the sclera is a firm, dense, fibrous membrane. It cannot be separated into lamellæ, as its fibrous bundles are intimately interwoven, crossing mainly at right angles, running in meridional and equatorial directions, those having the former course being seen mostly on the surface and behind, those of the latter around the cornea. Advantage is taken of this

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in incising the sclera, a meridional cut being usually preferred if at some distance from the cornea, as it is less likely to gape. The tendons of the recti muscles reinforce the sclera with meridionally directed fibres, while those of the oblique muscles become equatorial. In both cases the fibres penetrate obliquely through the entire thickness of the tunic. Near the posterior pole (region of the fovea centralis) there is found a strand of fibres that penetrates obliquely all the layers. This is called the *funiculus scleræ* by Hannover, who held it to be a cicatrix showing where the chorioideal fissure of fœtal life closed up. Schwalbe concludes, after careful examination, that this is not the true interpretation of the structure, but that it is merely a strand of connective tissue that accompanies the posterior ciliary arteries. Ammon[1] has described in the sclera, as well as in the deeper tunics of the eye, some traces of the primitive chorioideal fissure, and has named them the *raphe scleræ*. Whenever the sclera is cut, the cicatricial tissue that forms at the wound is of an irregular character, and may readily be distinguished from the other portions of the membrane.

Between the interwoven bundles lie lacunar spaces, like those of aponeurotic membranes, constituting an intricate and extensive system of lymphatic canaliculi that communicate on the one hand with the perichorioideal space, on the other with the perisclerał space. Some of these lacunæ are lined with endothelium.

It is mostly by this lymphatic circulation that the sclera is nourished, for it is very scantily supplied with blood-vessels. A few branches from the ciliary arteries penetrate its substance, forming a large-meshed capillary net-work. Each artery is usually accompanied by two veins. As a consequence of this scanty blood-supply, the sclera is but little disposed to inflammation, operations upon it are usually attended with favorable results, and it bears sutures very well.

Near the corneal margin there runs in the deeper portion of the sclera a passage concerning which much controversy has arisen. This is the *scleral sinus* or *canal of Schlemm*, which may be described as an overflow channel surrounding the cornea. It is connected with the venous system, but is also described as a lymph-space. It appears to be empty under ordinary conditions. When intra-ocular pressure is increased, it affords some relief by acting as a conduit of discharge. Its minute description and connections will be given later.

The nerves of the sclera are derived from the ciliary nerves. Within the substance of the tunic they first lose their medullary sheaths, then break up into fine fibrillæ that appear to end, like the nerves of the cornea, in pointed filaments between the bundles of the connective-tissue fibres. The investigation of the scleral nerve endings by modern methods offers a promising field.

In its chemical characters the sclera resembles other fibrous tissues in

[1] Präger Vierteljahrsschrift, 1860, i. 140.

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that it yields gelatin upon boiling. Wagner found that the fresh sclera of the pig yielded 65 per cent. of water and .867 per cent. of ash.

THE CORNEA.

As object-glass of the ocular camera, the cornea[1] is one of the most important portions of the apparatus. Being necessarily placed at the front, and exposed whenever the eyelids are parted, it is more frequently injured than any other part of the eye. In occupations in which small flying particles abound, such as grinding, stone-cutting, and some forms of iron-working, fragments often impinge upon it or bury themselves in its substance, requiring for their removal operative interference.

Perhaps the most striking property of the cornea is its almost perfect transparency. This is so nearly complete that under ordinary conditions we are quite unconscious of any obstacle to the passage of light. When viewed obliquely or under a strong light, the cornea may, however, be seen, as some reflection then occurs from the individual fibres. It seems astonishing that a membrane of so complex a constitution should be transparent, composed as it is of a stroma of connective-tissue fibres in several layers, lined in front and behind with epithelium resting on a basement membrane, having also within its substance two kinds of cells, a complicated system of lymph-passages, and an intricate, close-meshed plexus of nerves.

Evidently all these structures must be transparent. But it is well known that a mixture of transparent substances intercepts the light, the rays being thrown out of their direct course and diffused by passing from one to another. Thus, while a sheet of pure ice is transparent, it becomes opaque when broken into fine fragments, being then intermingled with air, which has a different refractive power. By adding water to the fragments, transparency is partially restored, the index of refraction of water more closely approaching that of ice.

The elements of the cornea must, therefore, have about the same refractive power. Are they also aided by the interposition of some fluid medium? It was formerly thought that this was the case, and that transparency was insured by an infiltration of the aqueous humor from the anterior chamber of the eye. This is, however, so far from being true, that when an infiltration does occur by reason of a lesion of the epithelial lining of the chamber, or, after death, by a change in the osmotic action of the membrane, the cornea speedily becomes clouded. Besides, when desiccated so that no fluid remains between its elements, it still retains its transparency.

The interposition of a fluid medium is, therefore, unnecessary. Why, then, are not the rays diffused as they are by the fragments of broken ice? If those fragments could be replaced in their relative situations with no film

[1] From L. *corneus*, *-a*, *-um*, horny. Syn.: *cornea pellucida*. Galen's term for the cornea was *κερατοειδὴς χίτων*, horn-like tunic, from *κέρας*, *-ατος*. From this is derived the term keratitis for inflammation of the cornea. Hyrtl points out that the term should properly be keratoiditis.

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of extraneous matter intervening, it is evident that the transparency of the mass would be fully restored.

It is easily shown that the transparency of the cornea depends on such a close and intimate contact of its elements, for any action that tends to disarrange or displace these elements produces an opacity. If, for example, a perfectly fresh eye be compressed between the thumb and the finger, the cornea immediately becomes clouded, returning to its natural condition when the pressure is removed. This also occurs when the membrane is compressed between plates of glass or when it is stretched by any means. In acute inflammations of the eye the pressure caused by engorgement of the vessels is likely to produce some opacity. At birth the cornea is hazy, and it also becomes clouded immediately after death, owing to a lessening of intra-ocular tension. Gerlach holds that the slight variations of tension that occur during perfect health have an effect upon the transparency of the cornea, that the brilliant sparkle noted in emotional excitement and during fever is due to the increased tension effecting a more accurate readjustment of the elements, and that a decrease of tension causes the dimness of the eyes under depressing emotions and during failure of bodily powers.

Slight variations in transparency due to other causes may also occur. The conjunctiva that lines the outer face of the cornea is an epithelial membrane whose cells desquamate and are shed off as in other cuticular structures. The desquamated cells, scattered like dust upon the exposed surface, temporarily dim the sight until washed away by the lacrymal secretion. Collections of such cells may appear in the field of vision as floating specks, or *muscæ volitantes*. The slight dimness which is noticed upon opening the eyes after sleep, and which causes an inclination to rub them, is due to such a collection.

The index of refraction of the cornea is stated by Krause as 1.3523, that of distilled water being 1.3358.[1]

Some interesting experiments have been made to determine the behavior of the cornea with regard to the rays of the invisible portions of the spectrum. Its power of absorption of the infra-red or heat rays is a little superior to that of water, but not notably so. The retina, therefore, appears to be remarkably insensitive to heat rays, as there is no obstacle that prevents their reaching it. The chemical or ultra-violet rays also appear to pass through the cornea without sensible diminution. There is some absorption of blue rays, as light that has passed through the cornea colors an alcoholic solution of guaiacum a yellowish green.

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[1] Krause (W.). Die Brechungsindices der durchsichtige Medien des menschlichen Auges, 1855.

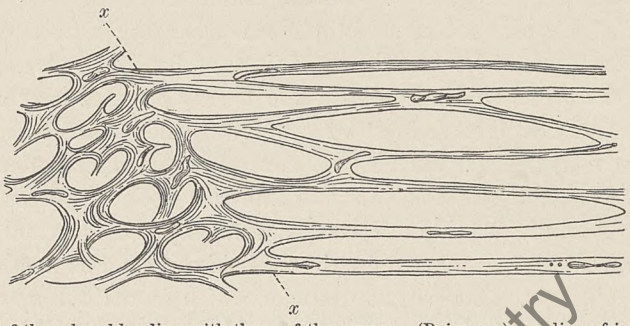
Other authorities have given the index as follows: Charles Chossat, 1.33 (Bull. Soc. philomath. de Paris, 1818, p. 95); Aubert, 1.377 (Gräfe und Sämisch, Handb. der gesammten Augenheilkunde, ii. p. 409); L. Matthiessen, 1.3754 (Archiv f. die gesammte Physiologie, xix., 1879, p. 492); A. Macalister, 1.3825 (Text-Book of Human Anatomy, 1889, p. 668).

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The cornea is set in the bevel of the corneal interval, already described. Its tissue does not suddenly cease at its circumference, but intimately interblends with the sclera. (See Fig. 22.) It appears to project from the latter, the amount of such projection being 2.7 millimetres (Merkel[1]), measured from a chord drawn at its base.

The curvature of its anterior or exposed surface is not quite regular, being that of an irregular ellipsoid whose radius in the horizontal meridian is 7.8 millimetres, while in the vertical meridian it is but 7.7 millimetres. (Donders.) The variations may, however, be much greater than these. In consequence of this asymmetry, rays proceeding from any point of an object are not all accurately focussed to a corresponding point of the retina, and a defect of vision known as astigmatism results. This occurs to a slight degree in every eye. Leroy[2] examined the eyes of fifteen cuirassiers of about the same height, physiological habits, and education, all possessing

FIG. 22.



Fibres of the sclera blending with those of the cornea. (Bowman.) *x x*, line of junction.

vision nearly or quite perfect, taking five points, one at the centre, the others nineteen degrees from the centre, above, below, to the right, and to the left. At each of these he measured the curvature of the horizontal and vertical meridians. He found that the curvature diminished from the centre of the cornea to its periphery, and was less on the temporal side than elsewhere. Considering the temporal flattening as unity, the flattenings above and below would be two and the nasal flattening four. The maximum flattening is found in that part of the cornea nearest to the insertion of the rectus medialis, which is much stronger than the other muscles of the eye. He holds that the unequal action of the eye muscles is the main factor in producing the asymmetry of the cornea.

The curvature of the posterior surface appears to be more regular and to approach that of a sphere having a radius of six millimetres. (Merkel.[3]) Careful observations with the ophthalmometer show that the contraction

[1] Macalister, op. cit., gives this as 2.6 millimetres.

[2] Leroy (C. J. A.). Sur la forme de la cornée humaine normale. Comptes-rendus de l'Acad. des Sciences, Paris, 1888, cvii. 696, 697.

[3] Macalister, 6.7 millimetres.

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of the muscles of the eye in no way affects the curvature of the cornea, and that accommodation for near and remote vision cannot be affected by it.

Since the outer and inner surfaces are not similarly curved, it follows that they cannot be parallel, and the cornea must vary in thickness. It is somewhat thicker than the sclera, averaging .9 millimetre at the periphery. (Merkel.[1]) Abscesses are more likely to perforate the membrane at its thinner portion.

The cornea attains its permanent dimensions very early, and varies but little after the third year. It appears, therefore, that accurate sight is of so much importance to the young animal that the development of that organ is hastened much beyond that of the rest of the body. It has been very aptly said by Priestley Smith[2] that as the brain develops faster than the general mass of the body, so the eye develops faster than the brain and the cornea faster than the rest of the eye. Petit states that the absolute thickness of the cornea is greater at birth than at any other time of life. In young children it is frequently thicker at the centre, and to this has been ascribed the short-sightedness common among infants. The cornea is of slightly smaller diameter in females (.1 millimetre). Its size has no relation to its refractive powers, it being no larger in myopic than in emmetropic eyes. It appears to attain its full growth so early that it is not affected by any subsequent alterations in the posterior hemisphere. It may undergo a slight diminution in size in old age.

In elderly persons there is usually seen a narrow gray or yellowish-white crescentic line, either at the lower or the upper border of the cornea, concentric with the limbus. This is the *arcus senilis*,[3] and is due to a finely granular infiltration of hyaline substance. It usually appears first at the upper portion.[4] Somewhat later a similar arch is formed opposite to the first at the lower border, and these finally unite, forming a complete ring, wider above and below than on the sides. (See Fig. 23.) Its outer edge is usually sharp, a clear space existing between it and the limbus, while on the inner side it fades gradually away. Sometimes, however, there is an outside line that appears as if the sclera were impinging unusually on the cornea, then a clear space, followed by a second ring.[5] It never interferes with vision, although it may extend some distance towards the centre. It

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[1] The following measurements are given by others:

	Central.	Peripheral.
Testut	.8	1
Schäfer (Quain's Anatomy)	.8	1.1
Macalister	.9	1.12
Gerlach	1.1–1.2	1.2–1.3

[2] Smith (Priestley). The Size of the Cornea in Relation to Age, Sex, Refraction, etc. Lancet, 1889, ii. 1062.

[3] Syn.: *gerontoxon* (Gr. *γέρων*, old man, and *τόξον*, bow, arch); *macula arcuata* or *corneæ*; *marasmus senilis corneæ*; *annulus senilis*.

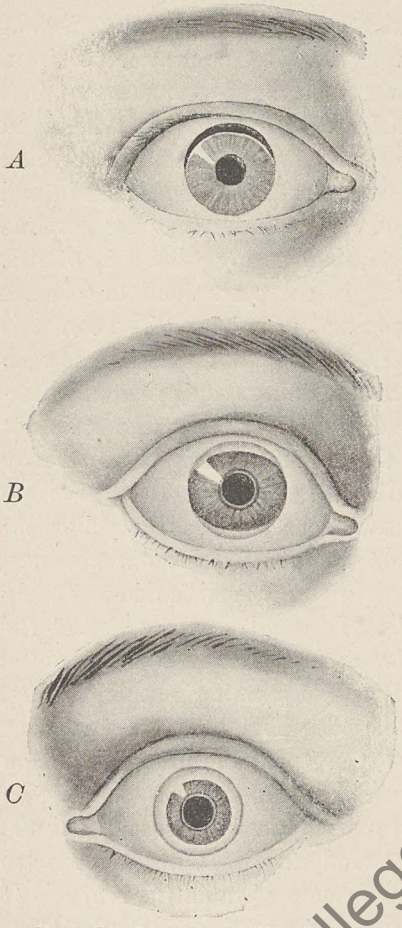
[4] Canton (E.). On the arcus senilis, London, 1863.

[5] Testelin (A.). Dict. encycl. des sciences médicales, Paris, 1867, vi. 4.

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is occasionally seen in young persons, even at the ages of six, eight, and ten years,[1] but is rare before fifty, and frequently absent until sixty years of age. It is more frequent and earlier in men than in women, and its early development appears to be hereditary. Canton figures five members of a single family, aged respectively eighteen, twenty, twenty-five, fifty-three, and fifty-six, all possessing the arch in some form, the two last—the father and mother—having complete circles. In warm climates it is developed earlier than in cold latitudes: at least it is more frequently seen in negroes of the north coast of Africa.[2] It is usually simultaneously and symmetrically developed in both eyes. It is commonly said that it is due to fatty degeneration or infiltration of the cornea, but Fuchs has shown that this cannot be the case.[3] He found that the infiltrated material never has any relation to the cells of the corneal tissue, but is free upon the surface of the connective-tissue fibres. Neither ether nor chloroform has any effect upon it, so it is certainly not of a fatty nature. He believes it to arise from a hyaline degeneration of certain fibres. The arcus senilis appears, therefore, to be a normal phenomenon occurring in perfectly healthy subjects, due to the decrease of nutrition concomitant with advancing years, and has no relation, as was formerly supposed, to fatty degeneration of the heart.

Fig. 23.



Examples of the arcus senilis. (Canton.)—*A*, upper arch; *B*, upper and lower arches; *C*, complete ring.

Gruber[4] seeks to explain its occurrence in this restricted area by the peculiarities of circulation in the cornea. The peripheral zone he thinks is nourished mainly by transudation of nutritive materials from the circumcorneal plexus, and as age advances and the circulation is less active this nutrition is more feeble and degeneration ensues.

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[1] Woodman (W. B.). St. Andrew's Med. Grad. Assoc. Trans., Lond., 1872–73, vi. 144.

[2] Furnari. Voyage médicale dans l'Afrique septentrionale, Paris, 1845.

[3] Fuchs (E.). Zur Anatomie der Pinguecula. Archiv für Ophthalmologie, Leipzig, 1891, xxxvii., Abth. iii., 154, 155.

[4] Gruber (R.). Die Entstehung der Greisenbogens der Hornhaut. Wien. med. Wochenschr., Jahrg. xxiv., No. 24.

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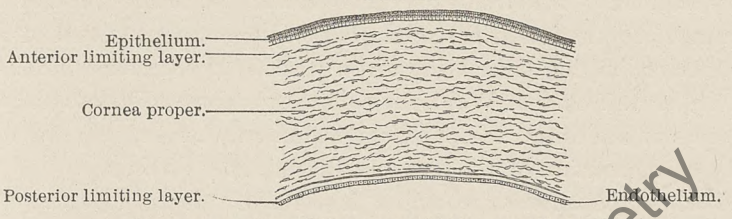
He thinks the middle of the cornea depends for nutrition upon the vital force of the cells themselves, causing an intercellular flow of lymph. This force remains about equal during life: hence these cells do not degenerate.

The average weight of the cornea is, according to Huschke, about one hundred and eighty milligrammes, or one-fortieth of the weight of the entire eye. Its specific gravity is stated by Davy to be 1.076.

The cornea does not, like the sclera, yield gelatin on boiling, but rather a special form of chondrine, called by Michel and Wagner corneo-chondrine. It also contains globuline and albuminoid substance, and 72.75 per cent. of water. The ash yielded is but 0.66 per cent.

Like the sclera, the proper substance of the cornea is composed of closely woven bundles of white fibrous tissue, arranged, however, in more distinctly separated lamellæ. Owing to its peculiar situation at the front of the globe, and to the fact that it here constitutes the entire thickness of the capsule, it comprises certain additional structures, the fibrous tissue being lined on either side by a clear structureless layer on which rests an epithelium. (See Fig. 24.) There are, then, from without inward, five well-marked layers, as follows:

FIG. 24.



Transverse section of the cornea, slightly magnified. (Gerlach.)

1. The external epithelium, a continuation of the conjunctival epithelium already mentioned.
2. The anterior limiting layer.
3. The cornea proper.
4. The posterior limiting layer.
5. The internal epithelium, or endothelium lining the anterior chamber.

These layers do not have the homologies that their situation and appearances indicate. The anterior and posterior limiting layers are by no means of the same nature, nor is the conjunctival epithelium strictly comparable with that lining the anterior chamber.

Attempts have been made to classify the layers according to their embryological history. Kessler[1] holds that the first trace of the cornea is a structureless sheet of epithelial origin developed between the epidermis and the lens, and that into this connective-tissue elements extend as a secondary phenomenon, the anterior and posterior limiting layers being the remains of this fœtal condition. This view, however, is erroneous. Kölliker[2]

[1] Kessler (Leonhard). Entwickelung des Auges der Wirbelthiere, Leipzig, 1877.
[2] Kölliker (Albert). Entwickelungsgeschichte, 2d edition.

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failed to find either membrane in a fœtus of ten days, and even at birth the posterior one cannot be discovered. Indeed, the posterior limiting layer increases in thickness with age, which does not seem likely to be the case with the relic of a fœtal structure. The original structureless sheet appears to be a mesenchymic blastema derived, like other similar elements, from the mesoderm.

Waldeyer,[1] basing his conclusions upon the observations of Manz and Lorent, holds that the corneal tissue is derived from three sources: an anterior or conjunctival portion, comprising the anterior epithelium, the anterior limiting layer, and a small portion of the cornea proper; a middle or scleral portion, comprising the remainder of the cornea proper; and, finally, a posterior or chorioideal portion, consisting of the endothelial lining, the posterior limiting layer, and some parts of the middle coat that interpose between the cornea proper and the posterior limiting layer.

Some objections have been made to this view. While there is no doubt that the epithelium of the anterior surface is a continuation of the conjunctival epithelium, it is doubtful if the anterior limiting layer can be considered as a continuation of the subepithelial layer of the conjunctiva. In some fishes, especially in Petromyzon (Langerhans, W. Müller), nearly the entire cornea is conjunctival, the scleral part being not represented at all, and the posterior limiting layer lying directly upon the anterior epithelium. Again, Kölliker thinks that Waldeyer's observers have mistaken for the posterior layer of the cornea the pupillary membrane, a thin, very vascular sheet lying on the surface of the lens and first sharply distinguished from the cornea when the anterior chamber is formed. It is, however, well known that the endothelium lining the posterior surface of the cornea is a continuation of that lining the anterior surface of the iris, which is considered of chorioideal origin; and the posterior limiting layer is, as will be hereafter shown, a product derived from the endothelial cells.

According to the most recent views on the subject, the following classification, which is essentially that of Schwalbe,[2] gives the correct morphological relations of the layers.

Classification of the Layers of the Cornea.

A. Cutaneous Portion.
   I. *Conjunctival Cornea.*[3]
      1. External epithelium.
B. Capsular Portion.
   II. *Scleral Cornea.*[4]
      2. Anterior limiting layer.
      3. Cornea proper.

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[1] In Gräfe und Sämisch's Handbuch der gesammten Augenheilkunde, vol. i.
[2] Schwalbe (G.), Sinnesorgane, 1887.
[3] Syn.: *pars conjunctivalis*, or *cutanea corneæ*.
[4] Syn.: *pars scleralis corneæ*.

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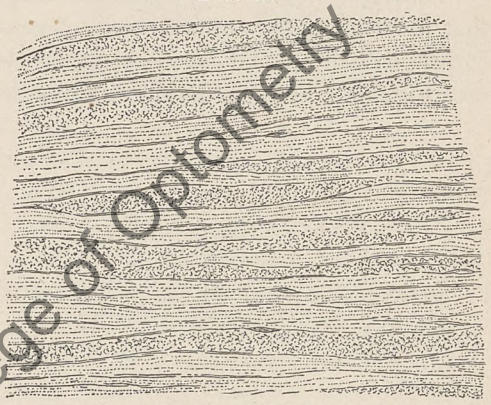
III. *Chorioideal Cornea.*[1]

4. Posterior limiting layer.
5. Internal endothelium.

The *cornea proper*[2] constitutes the main substance of the capsule, giving it strength and character. It forms a direct continuation of the sclera, and is composed of from sixty to sixty-five layers of flattened bundles of white fibrous tissue. It has long been known to be lamellated, even Avicenna (A.D. 980 to 1036) having been aware of the fact. (Merkel.) This lamellar arrangement should be remembered when operating, as the point of the instrument may engage between the layers and be diverted from its course if the knife is not properly held and the cut firmly made. It requires, as Hyrtl expresses it, some boldness to pierce properly the cornea.

The arrangement in lamellæ may be demonstrated by dissection, as one thin flap after another may be raised or torn up, not, however, without leaving a rough surface beneath. It is also displayed in cases where inflammatory action has partially disintegrated the cornea, as at the border of an ulcer, the edges of the lamellæ then turning up like the leaves of a dog's-eared book. In some of the lower animals the lamellæ are more distinct than in man: in the frog, for example, they run from side to side almost without interruption. In the human cornea the bundles composing the lamellæ are not all parallel, some of them passing into other levels at very oblique angles. The breaking of these occasions the rough surface already mentioned as seen when the lamellæ are forcibly separated.

FIG. 25.



Section of the cornea of an ox, highly magnified, showing the arrangement of the lamellæ. (Ranvier.)

A section shows that the bundles of contiguous layers are arranged in a crib-like manner, being nearly at right angles, so that when the fibres of one show longitudinally those of the other are cut transversely. (See Fig. 25.) The arrangement is not quite rectangular, there being a deviation to the right of some six degrees or more, so that the bundles of the first and third layers are not parallel, nor those of the second and fourth, etc. When the objective of a microscope used for examining the structure is slowly raised or lowered so as to focus in turn the successive layers, the bundles appear to revolve like the spokes of a wheel. The

[1] Syn.: *pars uvealis*, or *chorioidealis corneæ*.

[2] Syn.: *substantia propria corneæ; substantia fibrosa corneæ;* stroma of the cornea; fibrous layer of the cornea; lamellated tissue of the cornea (Bowman); lamellated cornea; mesocornea (Leidy).

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more superficial lamellæ differ somewhat from the others, being slightly thinner and more interwoven. They are also interpenetrated with the arcuate fibres[1] derived from the anterior limiting membrane.

It is well known that white fibrous tissue has the property of double refraction. Viewed through crossed Nicol prisms, it appears light upon a dark field if the axis of the fibres makes an angle of forty-five degrees with the plane of polarization. When a section of the cornea is placed in this way it shows a series of alternate light and dark bands corresponding to the lamellæ that are cut longitudinally and transversely. An entire cornea mounted with its convex side uppermost shows a dark cross on a bright field when viewed by polarized light. (His.)

The lymph-passages of the cornea have been for many years an object of investigation. The diverse views that have been held may be classified partially as follows:

1. They do not exist, the appearances cited in favor of them being artificially produced. (Sappey.)

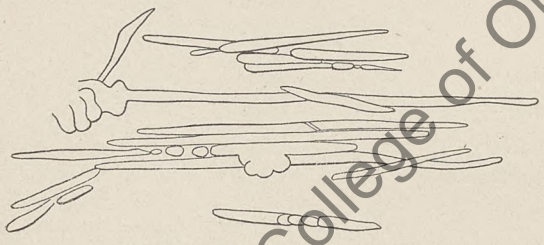
2. They exist, but are almost wholly filled with cellular elements. (Recklinghausen.)

3. They not only exist, but are completely lined with endothelial cells. (Hoyer.)

4. They are spaces partially lined, partially interlamellar and interfascicular. (Schwalbe, Gutmann.)

Among the earliest to investigate this subject was Bowman, who found that upon injecting mercury under a gentle pressure into the edge of the cornea, certain tubular passages appear which he called the *corneal tubes*. (See Fig. 26.) These generally run parallel to each other and to the lamellæ, but may lie obliquely or diverge in various directions, like the cracks in a shattered pane of glass. They are sometimes moniliform, and always have pointed extremities. The whole cornea may be filled with such tubes. They do not communicate with the lymphatics or other vessels, and when the fluid that fills them escapes it is usually into the anterior chamber. When too strongly urged, it parts the contiguous lamellæ, forming flat, irregular patches. An injection of atmospheric air answers quite as well as one of mercury. As these tubes are easily seen by the naked eye, it seems hardly probable that they relate to the minute structure of the cornea. In fact, sections show that they have no proper wall,

FIG. 26.



The "corneal tubes." (Bowman.)

[1] Syn.: *fibræ arcuatæ* (Schwalbe); *fibres suturales* (Ranvier).

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and that they are probably caused by a mechanical separation of the fasciculi in the various lamellæ.

The question, therefore, arises whether there are in the cornea any other structures that indicate lymph-passages. Toynbee, in 1841, discovered in the cornea certain appearances which he supposed to be cells. These were likened by Virchow to the osteoblasts or bone-corpuscles which occupy the lacunæ of osseous tissue, and were accordingly named the corneal corpuscles. When His and von Recklinghausen invented silver staining,[1] this view appeared to be confirmed. The cornea was the first object upon which the new method was used. The application of the solid stick produced a dark ground upon which light spots of a peculiar pattern appeared, these spots corresponding apparently with the corneal corpuscles. This was the so-called "negative" picture. (See Fig. 27.) A longer exposure with dilute solutions produced a pattern the reverse of this, the spaces being deeply stained while the ground remained comparatively light. This was the "positive" picture. (See Fig. 28.)

Fig. 27.



Cornea of a frog stained so as to show the "negative" picture. (Ranvier.)

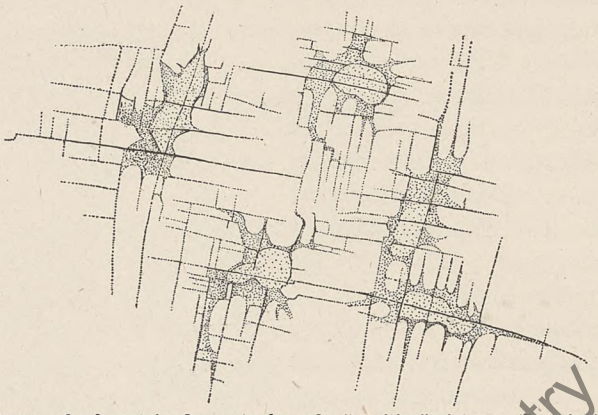
In opposition to Virchow's theory that these appearances are produced solely by the corneal corpuscles, von Recklinghausen held that they are caused by an intricate system of lymph-lacunæ (Saftlücken), connected with each other by delicate canaliculi (Saftcanälchen). He was led to this view by observing that wandering lymph-cells pass with great ease throughout the substance of the cornea. If a negative silver-stained cornea be placed within the dorsal lymph-sac of a living frog and allowed to remain a few days, it is found that leucocytes in great numbers penetrate it and are seen within the white passages. He therefore distinguished in the cellular elements of the cornea two classes,—the *fixed* cells that lie in the lymph-lacunæ, and the *wandering* cells that pass from place to place along the canaliculi. As a confirmation of this theory, C. F. Müller found that by injecting the cornea very carefully, approaching more nearly the physio-

[1] The first employment of nitrate of silver was apparently made by Finzler, who worked under the direction of Coccius. (See his dissertation, "De argenti nitrici usu et effectu, præsertim in oculorum morbis sanandis," Leipzig, 1854.) He noted the corneal corpuscles, but believed them to be produced by the corrosive action of the salt. It appears that His used the solid pencil as early as 1857 for developing the structure of the cornea; but the earliest publication of any exact use of the substance for histological purposes was made by von Recklinghausen in an article in the Archiv für pathologische Anatomie und Physiologie, 1860, xix. 451, entitled "Eine Methode mikroskopische Höhle und solide Gebilde von einander zu scheiden." He used solutions.

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logical conditions than Bowman did, it is possible to fill the lymph-lacunæ without causing such a separation of the fibres as leads to the formation of the corneal tubes. An intricate net-work of connecting passages is thus made out differing totally from the tubes. More recently, Gutmann,[1] by using asphalt dissolved in chloroform, has been able to show this, even in the cornea of the ox, which was thought not to contain them. This net-work agrees in its general plan with that developed by silver staining, but the passages are somewhat wider, owing probably to a slight distention from the injection. They increase slightly in size from the superficial to the deep layers, being largest near the posterior limiting membrane.

Fig. 28.



Cornea of a frog stained so as to show the "positive" picture. (Ranvier.)

Other methods of demonstration have also been used, so that at present it can hardly be said that the existence of lymph-passages is open to doubt.

It must, however, be admitted that if we seek for distinct vessels provided with a definite wall, they are not found in the cornea. The passages appear to be rather interfascicular spaces than true vessels, the adhesion of the fascicles to each other, at no time very great, being here wanting entirely. The fixed cells of the cornea, which are believed to be adherent either to one side or the other of the canals, offer the only trace of endothelial lining such as usually exists in the lymphatics of connective tissue, as, for instance, in the sclera. This lining appears, however, to be incomplete.

It is instructive to compare the intimate structure of the cornea with that of bone. In both there are laminæ, between which lie spaces or lacunæ interconnected by delicate canaliculi. Even the perforating fibres of bone appear to be represented by the sutural fibres of the cornea. It should be remarked, however, that these resemblances may be merely accidental. The osteoblasts of bone appear to have no analogue in the cornea, as the corneal corpuscles to which they were formerly compared are now

[1] Gutmann (G.). Ueber der Lymphbahnen der Cornea. Archiv für mikroskopische Anatomie, 1888, xxxii. 593.

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believed to be a composite product made up of the fixed corneal cells and a certain amount of infiltrated material.

At the edge of the cornea its lymphatic net-work communicates with that of the sclera, the difference in calibre of the passages being such that fluid more readily passes into than away from the cornea. Through the anterior limiting membrane the lymph penetrates along the nerves by special passages—the perineural canals—formed in the connective tissue of their sheaths, thus reaching the system of lacunæ that exists in the anterior epithelium, particularly between the "prickle-cells" of the deeper layers. From this it passes into the well-marked lymph system of the scleral conjunctiva. Fluid also reaches the net-work by osmosis from the anterior chamber. The interchange here is active, as shown by the rapidity with which diffusion takes place when special fluids are injected into the chamber. The quantity of fluid in the chamber remains about the same, and but little exudation appears on the anterior surface, even when the intra-ocular pressure is notably increased.

The *external epithelium* of the cornea[1] resembles in many respects the epidermis of the general surface of the body, being stratified in from six to eight layers, and rapidly renewed from the basement layer. It is somewhat thicker at the periphery than at the centre. Leber thinks that it has an important office in preventing the diffusion of tears into the general substance of the cornea. It is quite soft, and easily removed by knife or needle. In reptiles, that shed their skin entire, this epithelium is cast off with the external cuticle.

The *anterior limiting layer*[2] is clear, homogeneous, and anhistous,—that is to say, without apparent structure. It offers such resistance that particles of steel or other angular fragments often stick just within the surface of the cornea. It differs greatly in different animals, being absent in some, such as the horse, goat, dog, and cat (His), but in man, ruminants, and birds being well developed. At five years of age it is about equal in thickness to the posterior limiting layer; after that the latter gains upon it. It passes insensibly into the cornea proper, from which it is separated with difficulty. If any part is torn away, it rolls up so that the attached or deeper surface lies inward in the roll. If destroyed by inflammatory processes, it is never renewed. It thins away and is lost from one to one

[1] Syn.: *conjunctiva corneæ;* corneal conjunctiva; corneal epithelium; ectocornea. (Leidy.)

[2] Syn.: Bowman's membrane (for Sir William Bowman, Professor of Physiology in King's College, London, born 1816, died 1892, being described in his Lectures on the Parts concerned in the Operations on the Eye, London, 1849); anterior elastic lamina (Bowman); *lamina elastica anterior;* membrane of Reichert (for Karl Reichert, 1811–1883, who discovered it at about the same time as Bowman); *vordere Grenzschicht*, G. (Reichert); anterior homogeneous lamina; anterior or external basement membrane; *äussere* or *vordere Basalmembran*, G. (Henle); *subepitheliale Schicht*, G. (Arnold); *stratum nervosum* (Cohnheim, under the erroneous impression that it is mainly composed of an intricate plexus of nerve-filaments).

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and a half millimetres from the edge of the cornea, where the marginal looped plexus of blood-vessels begins.

Bowman, the discoverer of this structure, describes its union with the subjacent tissue as follows:

"The manner in which the anterior elastic lamina is united to the lamellæ which it serves to cover is very interesting. It must be borne in mind that the anterior surface of the cornea is convex, and that the maintenance of its exact curvature is of primary importance to vision, as it is there that the first inflexion of the rays of light falling in the eye takes place; and, further, that the conjunctival epithelium, being a soft and fragile substance, must take the figure of the surface on which it rests: hence, probably, the arrangement I am about to mention. The anterior elastic lamina, a firm, resisting, uniform layer, placed in front of the more soft and porous lamellated tissue, is tied down to the anterior lamellæ, at innumerable points, by filaments of similar texture to itself,[1] which it sends in among them. These, as they penetrate the lamellæ, divide and expand in such a manner as to take firm hold of them, and are thus gradually spent among the four or five lamellæ which lie nearest the surface. It is singular, too, that these filaments are not set vertically, but everywhere in a slanting direction among the lamellæ, so that in a vertical section they appear to cross one another at right angles. This arrangement might, I imagine, be shown on mechanical principles to be the best possible for the maintenance of the convexity of the front of the cornea."

The exact nature of this layer has long been a matter of discussion, and cannot yet be said to be entirely settled. As it is unaffected by dilute acids, Bowman supposed it to be similar to the elastic fibres of connective tissue, and therefore called it the anterior elastic lamina. The name is an unfortunate one, as the membrane, although elastic, is by no means identical in its reactions with elastic tissue. The latter may be colored by eosine, which leaves the former unaffected, and picrocarminate of ammonium stains the two quite differently. In boiling water and in liquor potassæ the anterior limiting layer swells up (Henle[2]), and permanganate of potassium breaks it up into fibrillæ that resemble those of the cornea proper (Rollett[3]). These reactions also distinguish it from elastic tissue.

Kessler's view that both the anterior and posterior limiting layers are the remains of the original blastema in which the cornea was developed has already been adverted to. The two differ so much in their chemical reactions that it seems impossible that they should have the same intimate constitution. For example, the anterior layer is not affected by a dilute solution of osmic acid, which stains the posterior layer brown; the former is colored bright red by picrocarminate of ammonium, which stains the

[1] In an annexed figure he styles these fibres "fibrous cordage."

[2] Handbuch der systematischen Anatomie des Menschen, 1873, ii. 629.

[3] Stricker's Handbuch der Gewebelehre.

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latter orange; hæmatoxylin stains the anterior layer very slowly, but at once imparts to the posterior one a characteristic violet hue.

The view most generally accepted is that the anterior layer is merely a condensed and somewhat modified limiting layer of the cornea proper, and Rollett's success in reducing it to fibrillæ is usually cited as conclusive evidence of this. It is difficult, however, to reconcile this view with the fact that acetic acid or dilute mineral acids do not affect this layer at all, while they at once cause ordinary white fibrous tissue, like that of the cornea proper, to swell up.

Ranvier[1] has shown that the cornea of the ray possesses an unusually thick anterior limiting layer, from which delicate prolongations (sutural fibres[2]) extend through the entire thickness of the cornea proper. These have the same reactions as the membrane itself, picrocarminate of ammonium tinging the entire system a bright rose color, while the corneal lamellæ remain unstained. In the human cornea traces of a similar system are found, the sutural fibres being represented by the oblique filaments so graphically described by Bowman.

Searching for an analogue for this tissue, he finds it in the circular and spiral fibres found in connective-tissue bundles, particularly those of tendons and of the arteries at the base of the brain. When these bundles are treated with acetic acid they swell up, but the fibres referred to remain unaffected and appear as circular or spiral constricting bands, giving the bundles a moniliform aspect. They are not found at equal distances or distributed according to any fixed law. In some cases it is thought that the substance of which these bands are composed was primitively a complete investment of the bundle and was broken into shreds by the swelling; in others, that they are the filamentous processes of stellate connective-tissue cells. The reactions of these bands appear to be identical with those of the anterior limiting layer. Ranvier therefore concludes that the cornea is to be considered as a flattened band of tendon-like connective tissue with a special envelope (the anterior limiting layer) and encircling bands (the sutural fibres). At the edge of the cornea he was able to trace the transition from the modified to the usual form.

The *posterior limiting layer*,[3] often called the membrane of Descemet, is

[1] Ranvier (L.). Leçons d'anatomie générale, année 1878–79; Terminaisons nerveuses sensitives: Cornée. Paris, 1881.

[2] The "fibrous cordage" of Bowman; *fibræ arcuatæ* (Schwalbe).

[3] Syn.: membrane of Descemet, *membrana Descemetiana* or *Descemeti* (for Jean Descemet, a physician of Paris, born 1732, died 1810); membrane of Demours, *membrana Demoursiana* or *Demoursi* (for Pierre Demours, an oculist of Paris, born 1702, died 1795); membrane of Duddell, *membrana Duddelliana* (for Benedict Duddell, an oculist of London, 1729); membrane of the aqueous humor or *membrana humoris aquei* (Descemet); *membrana pro humore aqueo; capsula aquea cartilaginosa* or *præaquosa; lame cartilagineuse* (Demours); posterior elastic lamina (Bowman); lamina elastica posterior; *innere Basalmembran* (Henle); internal basement membrane; vitreous lamella of the cornea; entocornea (Leidy).

A long controversy occurred with regard to the priority of discovery of this mem-

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distinguished from the anterior limiting layer by several notable peculiarities. Its different behavior with staining fluids has already been adverted to. It has a considerably greater resistance to alkalies and acids, as well as to boiling water. Indeed, it may be isolated by submitting the cornea to strong alkaline or acid solutions, which dissolve the other constituents while leaving the membrane of Descemet unaffected. Anatomical differences also are not wanting. It is thickest at the circumference, while the anterior limiting layer thins away towards the edge. Although closely united to the cornea proper, it may yet be detached by maceration, and then has a tendency to roll up, with the surface formerly adherent inward in the roll. It is more easily digested by trypsin than is elastic connective tissue. In ordinary preparations it appears as a perfectly homogeneous glass-like sheet without trace of cells or other structure. Some observers (Schweigger-Seidel) report that it shows a fibrillary striation after boiling in a ten per cent. solution of sodium chloride. When cut it crackles under the knife, and the edge of a fracture may be straight, curved, conchoidal, or stepped and irregular. An attempt to disassociate it causes it to break up in every direction, like glass, following no definite planes. From its general behavior, Schweigger-Seidel believed it to be composed of thin platelets.

In early fœtal life this membrane is absent, the endothelium lining the anterior chamber resting immediately upon the cornea proper. About the second or third month it appears as a very narrow stripe, presenting the same glassy appearance as in the adult. It increases in thickness with age, and in the latter years of life shows on its posterior surface numerous papillary eminences, isolated or arranged in groups. These are apparently due to a progressive but irregular growth. In view of these evidences of gradual development, Ranvier thinks that the membrane is a product of the endothelial cells that coat it.

Internal Endothelium.[1]—The layer of cells that lines the anterior chamber is often called an epithelium, but, as it is undoubtedly a form of connective tissue having an epithelioid character, it seems better to apply to it the

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brane. The first published mention of it by Descemet occurs in his dissertation "An sola lens crystallina cataractæ sedes?" Paris, 1758. Demours's first publication was in his Lettre à M. Petit, Paris, 1767; also in the Mémoires de l'Académie, 1768, page 177.

Some time prior to this, however, the membrane was seen and mentioned by Duddell, as appears from the following passage from his Treatise on the Diseases of the Horny Coat of the Eye, London, 1729: "I have found by the Dissection of Eyes Fibres both in the outward and inward Chamber; one was adherent to the Arachnoides [capsule of the lens], and another to the Cornea. I found a Film in a Horse's Eye, of a yellowish Colour, which swimming in the Aqueous Humour of the outward Chamber cover'd half the Pupil. I made an Incision in the lower Part of the Horny-coat with a Lancet, and putting a blunt Needle into the Orifice, I drew Part of it out; the other End was adherent, a little above and sideways from the Incision, and broke off almost by the Adherency: And examining the Film, I found that it was a little Pelicle, that had separated from the Cornea, excepting only where it stuck."

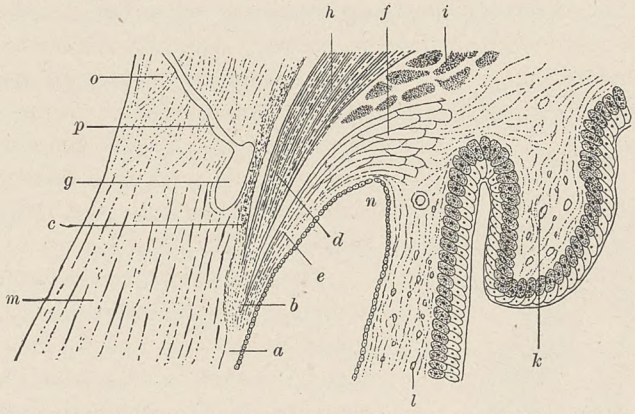
[1] Syn.: endothelium of the membrane of Descemet; internal epithelium of the cornea; epithelium of the membrane of Descemet; *epithelium humoris aquei.*

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name *endothelium*, invented by His for such tissues. It is composed of transparent, flattened, polygonal cells that have some peculiarities that will be mentioned under the section on histology.

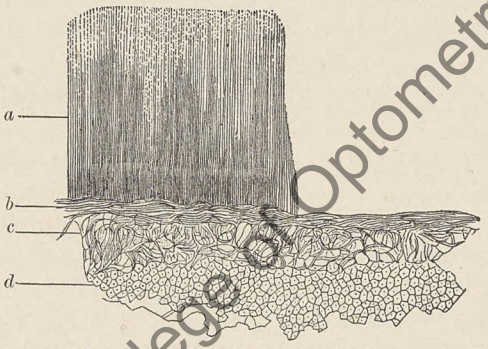
At the circumference of the cornea the posterior limiting membrane is thickened into a ring-like margin, the annular ligament.[1] From this

FIG. 29.



Meridional section showing the connection between the cornea and the middle coat of the eye. (Testut.)—*a*, posterior limiting layer; *b*, annular ligament; *c*, scleral fibres; *d*, ciliary fibres; *e*, posterior fibres forming the pectinate ligament; *f*, Fontana's space; *g*, scleral sinus; *h*, meridional fibres of the ciliary muscle; *i*, annular fibres of same; *k*, ciliary process; *l*, iris; *m*, cornea; *n*, angle of the iris; *o*, sclera; *p*, scleral vein.

FIG. 30.



A preparation made parallel to the surface of the annular ligament. (Gerlach.)—*a*, meridional fibres of the ciliary muscle; *b*, circular fibres of the annular ligament; *c*, longitudinal fibres of the annular ligament forming a reticulum in Fontana's space; *d*, posterior limiting layer, covered with the endothelial cells of the anterior chamber.

separate bundles of fibres, lying in three distinct planes, pass to the sclera, to the tendon of the ciliary muscle (hereafter to be mentioned), and to the iris. (See Figs. 29 and 30.) The strands of the latter group are known as the *pectinate ligament*.[2] The narrow region between the cornea and the

[1] Syn.: *ligamentum annulare; annulus tendinosus.*

[2] Syn.: *ligamentum pectinatum iridis* (Hueck); *processus peripherici;* pillars of the iris.

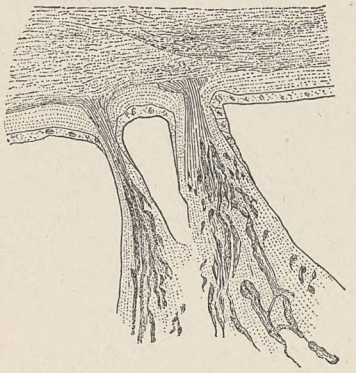
The name in the text is derived from L. *pecten, -inis*, a comb. In hoofed animals, in

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iris, near this ligament, is often called the *angle of the iris*,[1] and the region occupied by the bundles of the ligament the space of the angle of the iris.[2] The intervals between them are free from interstitial material, and communicate with the anterior chamber, being in fact a continuation of it. They are much better marked in the ox and horse than in man.

It will be perceived that the arrangement just described is such as to connect the membrane of Descemet rather with the middle coat of the eye than with the outer one, thus supplementing what has already been deduced from embryological evidence,—namely, that the membrane is derived from the middle coat. An examination of the strands of the pectinate ligament shows that each is coated by a continuation of the membrane of Descemet, and by an endothelial layer that grows thinner as it recedes from the cornea, the membrane also undergoing reduction. (See Fig. 31.)

FIG. 31.



Meridional section of rabbit's cornea, showing strands of the pectinate ligament. (Ranvier.)—The axis of the strands is formed of an extension of the tissue of the cornea proper; the cortex of them is an extension of the posterior limiting layer, and upon this extends an epithelial investment continuous with the endothelium of the anterior chamber.

The intervals of the space of the angle of the iris communicate with the lymphatic spaces of the iris, and by this way fluid may be carried directly from the anterior chamber into the lymphatic circulation.

Just without this space, within the precincts of the sclera, where the internal surface of that membrane bends inward before uniting with the tissue proper of the cornea,[3] there is found the curious passage or system of passages already referred to as the *scleral sinus*, or *canal of Schlemm*.[4]

This has in cross-section so much the appearance of one of the intervals of Fontana's space that it has been thought to be of the same nature and therefore to belong to the lymphatic system. It is

whom the structure was first observed, the arrangement in distinct bundles passing from the cornea to the iris is much more marked, and these appear, when viewed from the side of the chamber, like the teeth of a comb.

[1] Syn.: angle of the anterior chamber; irido-corneal angle; *Iriswinkel*, G.; *angulus iridis*.

[2] Syn.: space of Fontana, named for Felice Fontana, professor at Pisa and afterwards at Florence, born 1720, died 1805. Fontana, misled by the unusual development of this trabecular tissue in the eyes of kine, and probably making some error in manipulation, described it as a *canal*. The term "Fontana's spaces" is often applied to the numerous small intervals between the trabeculæ. This seems to be inadmissible.

[3] The internal scleral sulcus of Schwalbe.

[4] Named for Friedrich Schlemm, an anatomist of Berlin, born 1795, died 1858.

Syn.: *sinus sclerœ* (Rochon-Duvigneaud); *canalis* or *sinus Schlemmii*; *canalis Lauthi*; *plexus ciliaris* (Leber); *circulus venosus Schlemmii*, or *circulus Schlemmii* (Leber, 1895); *sinus venosus sclerœ*, or *sinus venosus Schlemmii* (Gutmann and Waldeyer, 1895); *sinus*

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lined with endothelium, and has a thin wall closely united with the scleral tissue. It is not in all places a simple canal, but divides at short distances into several branches, which again reunite. This has led some to designate it as a plexus. Where single, it is oval or triangular in section, having a long diameter of 0.32 millimetre and a short one of 0.048 millimetre. (Schwalbe.) There pass from it to the anterior ciliary veins small veinlets that receive branches from the ciliary muscle, and this has led to the theory that it acts as a reservoir for the blood expressed from that muscle during contraction.

Rochon-Duvigneaud[1] has called attention to the fact that this passage greatly resembles in structure the sinuses of the dura mater. Like them, it has an endothelial lining resting immediately upon the circumjacent tissue, and not, like the vorticose and other veins, upon a wall of its own, separated from the tissue in which it lies by an adventitia. There are also trabeculæ and fibrous crests within it that serve to subdivide it more or less completely. These peculiarities were noted by some of the earlier observers, who gave it the name of sinus.[2]

The exact nature of this sinus has been for many years a subject of dispute. As it is usually empty after death, it has been held to be a lymph-channel. This is supported by the evidence of some who showed that it may be filled either wholly or partially by colored injections made into the anterior chamber after death at about normal pressure. Schwalbe[3] succeeded in doing this with soluble Berlin blue, alkanet turpentine, and asphalt dissolved in chloroform; Heisrath[4] with sulphindigotate of sodium, eosine carmine, and defibrinated blood; Calori[5] with cinnabar and basic acetate of lead; Gutmann,[6] quite recently, with Japanese ink, Berlin blue, and defibrinated blood. The annexed figure (Fig. 32), taken from Gutmann's article, shows fine granules of the ink lying within the lumen of

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venosus iridis (Henle); *sinus venosus corneæ; circulus venosus iridis; sinus circularis iridis;* circular sinus (Leidy).

First discovered by Albinus, as is shown by a catalogue of his preparations, published in 1775. First described by Schlemm, in Rust's Handbuch der Chirurgie, Berlin und Wien, 1830, iii. 333. He states that he found it in the eye of a person who had been hung, and cautions against confounding it with Fontana's canal.

[1] Rochon-Duvigneaud. Recherches anatomiques sur l'angle de la chambre antérieure et sur le canal de Schlemm. Arch. d'ophth., Par. 1892, 1893, xii., xiii.

[2] Arnold (Fr.). Anatomische und physiologische Untersuchungen über das Auge, 1832, p. 10 *et seq.* Retzius, Ueber den Circulus venosus im Auge. Archiv für Anatomie und Physiologie, 1834, pp. 292–295.

[3] Schwalbe. Lehrbuch der Anatomie der Sinnesorgane, 1887.

[4] Heisrath. Ueber die Abflusswege des Humor aqueus mit besonderer Berücksichtigung des sogenannten Fontana'schen und Schlemm'schen Canals. Arch. f. Ophth., 1880, xxvi. 1.

[5] Calori. De' risultamenti ottenuti injettando i canali di Fontana e di Petit e la camera anteriore dell' occhio umano e dei mammiferi domestici. Mem. Accad. d. sc. d. Ist. di Bologna, 1874, 3. s., v. 341–351.

[6] Gutmann (G.). Ueber die Natur des Schlemm'schen Sinus und seine Beziehungen zur vorderen Augenkammer. Arch. f. Ophth., 1895, xli. 28.

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the sinus. These evidently penetrate by means of the space of Fontana, and then by some means through the walls of the vessel.

It has been held from these experiments that open passages exist in the walls by which fluids may reach the sinus. Schwalbe cites similar connections between the lymphatic vessels of the Pacchionian bodies of the arachnoid and the sinuses of the dura mater. He compares the space of the angle of the iris to a sponge that sucks up fluid from the anterior chamber and discharges it into the sinus. The action is aided, as he thinks, by the ciliary muscle, some of whose fibres are attached to the inner wall of the

FIG. 32.



Section of a preparation made by injecting India ink into the anterior chamber. (Gutmann.)—*s*, scleral sinus in which fine particles of ink are seen; *e*, portions of the injection mass passing from the neighboring tissues into the sinus; *b*, fusiform and acuminate collections in the spaces of the neighboring tissues; *r*, scattered granular masses of India ink.

sinus, so that each contraction of the muscle draws asunder the walls and thus induces a suction upon the space of the angle of the iris and through it upon the anterior chamber. The fact that increase of intra-ocular pressure at once causes a congestion of the anterior ciliary veins seems to favor this view. It is true, however, that no one has yet succeeded in showing the actual channels by which such a communication might be effected, and many experimenters have failed to obtain positive results from injections made in perfectly fresh eyes.[1]

Leber[2] has recently repeated his former experiments on this subject with

[1] See Staderini, Ueber die Abflusswege des Humor aqueus, Archiv für Ophthalmologie, 1891, xxxvii. 3. Gifford, Weitere Versuche über die Lymphströme und Lymphwege des Auges, Archiv für Augenheilk., 1893, xxvi.; Rochon-Duvigneaud, loc. cit.

[2] Leber (Th.). Der Circulus venosus Schlemmii steht nicht in offener Verbindung mit der vorderen Augenkammer. Arch. f. Ophth, 1895, xli. 235.

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a view to reconciling the conflicting evidence. He finds that the discordant results obtained by different experimenters can be explained by the different conditions prevailing and the different methods pursued. Freshness of material is an important element, as in a very short time after death the endothelial cells contract so that injections readily pass between them. Again, injections pass much more readily into the sinus when the anterior chamber has first been emptied of its contents. In the case of some of the liquids used,—Berlin blue, for example,—it is found that the aqueous humor determines a precipitate of fine flakes that cannot enter the vessels. A slight amount of rough handling causes the results to vary.

After exhaustively examining the whole matter, he concludes that injected fluids do indeed pass from the anterior chamber to the scleral sinus, not through open connections or by stomata, but by intercellular filtration. Dissolved coloring-matters not precipitated in the anterior chamber pass without difficulty, as do also fine, suspended granules, such as those of India or Japanese ink.

He also points out that this conclusion is supported by the ordinary experience of ophthalmologists. If fluids could leave the anterior chamber by distinct openings, a constant intra-ocular pressure could not be maintained, nor would that pressure ever be much greater than that in the veins. Considerable difference in pressure, however, often exists. Under normal conditions no influx of blood into the anterior chamber occurs when the aqueous humor is evacuated, yet it is difficult to understand how this could be prevented were there open communications between the chamber and any part of the venous system. The sinus usually is found empty after death, because the intra-ocular pressure does not immediately cease, and this causes a filtration of the aqueous humor which drives out the blood. The anterior ciliary veins share this peculiarity. After death by diseases of the most varied nature the sinus may be found filled with blood, as is shown by the investigations of Iwanoff and Rollett.[1]

Blood-vessels.—In the adult cornea there are no blood-vessels, except within a margin of one to two millimetres near the limbus, where the episcleral vessels end in a net-work of capillaries known as the *marginal looped plexus.*[2] During fœtal life this vascular net-work extends between the deeper layers of epithelium and the anterior limiting membrane much farther, and may overspread the entire anterior surface. The cornea of some osseous fishes is vascular throughout life. The substance of the cornea normally contains no vessels. During inflammation, however, vessels may form in any portion, usually commencing as an extension of the marginal plexus, just beneath the external limiting membrane, and extending from this into the deeper layers. In some cases a newly formed

[1] Iwanoff and Rollett. Bemerkungen zur Anatomie der Irisanheftung und des Annulus ciliaris. Arch. f. Ophth., 1869, xv. 54.

[2] *Randschlingennetz*, G.

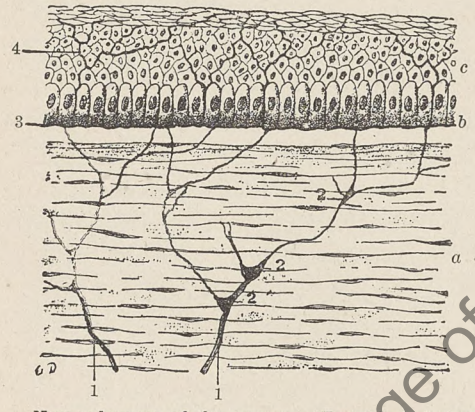
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tissue (*pannus*) is deposited upon the cornea. It should be noted that when the vessels are superficial they are plainly visible and have a vivid red color, branching in an arborescent manner; but when deeply situated they are not easy to make out, owing to the infiltrated and clouded layers covering them, and they divide into branches that run parallel to each other, or nearly so, along the corneal laminæ. (Fuchs.)

Notwithstanding the absence of blood-vessels, the nutrition of the cornea is very active, as is shown by the rapidity with which wounds are repaired, a day sometimes sufficing for healing when the conditions are favorable. This is probably due to the extraordinary copiousness of the lymph-supply, which here takes the place of blood. In wounds involving loss of substance the epithelium is renewed by proliferation from that surrounding the wound, but the tissue of the cornea proper is replaced by cicatricial tissue which never becomes perfectly transparent. The anterior limiting membrane is never renewed.

Nerves.—As might be expected from the highly sensitive character of the cornea, the nerves that supply it are exceedingly numerous. From the anterior ciliary nerves trunks pass that unite near the corneo-scleral junction to form a close-meshed plexus containing medullated and non-medullated fibres. From this plexus, known as the *plexus annularis*,[1] nerves pass to the ciliary muscle, to the iris, and to the cornea. Those that penetrate the cornea are of variable size, sixty to eighty in number, forty to fifty of which pass towards the anterior surface, while twenty to thirty are directed posteriorly. (Dogiel.) These nerves contain both medullated and non-medullated fibres, the former preponderating in the anterior set. The smallest of them have but two to three nerve-fibres, the largest have as many as twelve. Soon after entering they lose their medullary sheaths, thus becoming transparent, and exchange fibres with each other, forming a rich and intricate plexus, the *deep stroma plexus*.[2] (2, Fig. 33.) This extends like a net through the anterior three-fourths of the cornea proper, the posterior fourth being supplied by simple branches from it. Its strands are nerve-fibres, its intersections an almost

FIG. 33.



Nerve-plexuses of the cornea. (Testut.)—1, 1, two afferent nerve-trunks; 2, deep stroma plexus; 3, sub-epithelial plexus; 4, intra-epithelial plexus; *a*, cornea proper; *b*, anterior limiting membrane; *c*, anterior epithelium.

[1] Syn.: *orbiculus gangliosus*.

[2] Syn.: primary plexus; fundamental plexus.

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inextricable interlacement of these fibres mingled with some connective-tissue cells. No true ganglionic cells are found at these nodes.

The larger nerve-trunks are surrounded by special lymph-canals like those about the vessels, called the perineural canals. These are composed of two concentric endothelial sheaths enclosing between them a space that communicates with the interlamellar spaces of the cornea. The smaller branches appear not to have these special sheaths, but to lie immediately within the interlamellar spaces.

It was formerly thought that this plexus was, like those of the intestinal walls, a terminal plexus, from which were distributed the terminal nerve-filaments. This is, however, not the case. From that part nearest the anterior limiting membrane fibres are given off which pass in a radial direction, penetrating that layer (perforating fibres[1]) and then breaking up into fine filaments which unite beneath the epithelium in a close-meshed plexus, the *subepithelial plexus.* (3, Fig. 33.) Some of the perforating fibres do not enter this plexus, but terminate in the deeper layers of the epithelium in rounded or conical end-bulbs. (Dogiel.) From the subepithelial plexus, again, numerous varicose fibres pass between the epithelial cells and, gradually becoming more superficial, form an *intra-epithelial plexus.* (4, Fig. 33.) From this arise the terminal fibrillæ, which end in rounded or knob-like expansions.

Around the vascular edge of the cornea are found some peculiar end-organs, first described by Ciaccio,[2] and recently by Dogiel.[3] These are plexiform glomeruli of various shapes and sizes, formed by two or three nerve-branches that divide and subdivide. No cell-elements have been observed between the meshes of these glomeruli. Loop-like bendings with thickenings are also seen, especially in nerves that appear to enter from the circumcorneal tissue. Irregular quadrangular or shovel-shaped platelets are also found. These end-organs all appear to be confined to the exterior zone of the cornea, not occurring beyond one-half to one and a half millimetres from the edge.

Besides the deep stroma plexus and its derivatives, there is also found another, composed of finer fibrils, formed of branches derived from the main trunks, from branches of the principal plexus, from the perforating fibres, and from branches from the conjunctiva. This forms the *superficial stroma plexus,*[4] so called because most apparent beneath the anterior limiting membrane. It seems, however, from the researches of Dogiel, that it is by no means confined to this situation, as it ramifies extensively between the other layers of the cornea, so that each layer may be said to have a plexus of its own, except, indeed, the deepest near the posterior limiting membrane. Fibres from this plexus run along between the layers, frequently bend-

[1] Syn.: *fibræ perforantes; rami perforantes.*

[2] Ciaccio (G. V.). Mem. Accad. d. sc. d. Ist. di Bologna, 1873, ser. 3, iv. 501.

[3] Dogiel (A. S.). Die Nerven der Cornea des Menschen. Anat. Anz., 1890, v. 483.

[4] Syn.: subbasal plexus (Hoyer); accessory plexus (Ranvier).

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ing at right angles to communicate with those of the neighboring layers. They terminate by free ends slightly thickened or delicately tapering. It was formerly thought that they communicated with the corneal cells or with the so-called corneal corpuscles, but that has been shown not to be the case. They often pass over the surfaces of the corneal cells. These branches correspond quite closely to the corial branches of the cutaneous nerves.

Historically the corneal nerves are of considerable interest, as they were the first that were shown to end with free intercellular filaments. This method of termination is now known to be quite usual in the skin and mucous membranes.

THE MIDDLE OR VASCULAR COAT.[1]

Morphologically speaking, this coat extends from the optic-nerve entrance over the entire ball within the outer coat, being divided into four portions,—1, the chorioid proper, extending as far forward as the ora serrata, the place where the nervous portion of the retina ceases; 2, a thickened portion, the ciliary body, affording attachment to the suspensory ligament of the lens and containing within it plexuses of vessels and muscular fibres; 3, a freely hanging portion, the iris, that extends like a diaphragm across the aqueous chamber in front of the lens; 4, the corneal portion, already described as the posterior limiting membrane of the cornea, with its endothelium. This is usually excluded when reference is made to the middle

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[1] Syn.: *tunica media; t. uvea; t. uvæformis; t. aciniformis* or *acinalis; t. secundina; t. vasculosa; tractus uvealis; leptomeninx ophthalmencephali* (considering this coat as an extension of the combined arachnoid and pia mater of the brain).

The term *uvea*, often found in the older writers and occasionally employed by the moderns, has varied somewhat in its application. The earlier anatomists (Herophilus and others) compared the entire middle coat to the inside of a purple grape-skin, the pupil representing the place where the stem had been pulled out, and called it, therefore, *ῥαγοειδὴς χιτών*, or grape-like tunic (*ῥάξ* = L. *uva*, a grape). This was translated into Latin as *tunica uvea*, although, as Hyrtl points out, the name has no good etymological foundation, there being no adjective *uveus* derived from *uva*, a grape. The term was in general use for the entire middle coat until the seventeenth century, and there is a tendency among modern writers to return to it, as, for instance, Brücke (Anatomische Beschreibung des Augapfels, 1847), Luschka (Anatomie des Menschen, 1865), Helmholtz (Handbuch der physiologischen Optik, 1867), Pansch (Grundriss der Anatomie, 1891), and many recent writers on ophthalmology. Some of the older authors, however, applied the term to the iris alone. Rufus Ephesius, for example, calls the part of the middle coat to which the cornea is joined *ῥαγοειδὴς*, the posterior part *χοροειδὴς*. From the seventeenth century anatomists began generally to use the term in this sense. (See Riolanus, Petit, Winslow, Ruysch.) Later, Zinn, Haller, and Albinus restricted the term to the posterior layer of the iris, and it is now often so used. Haller uses the term in both significations. Morphologically, however, this is inaccurate, as the posterior layer is really a continuation of the retina. Schwalbe therefore calls the *anterior* layer of the iris its uveal portion.

The terms *uvæformis*, *aciniformis*, and *acinalis*, applied to this coat by old Latin authors, arise from the same comparison to a grape-skin (L. *acinus*, a berry or grape).

Gerardus Cremonensis, in his translation of Avicenna, applies to this coat the term *secundina*, partly because it is derived from the *secundina cerebri* (pia + arachnoid), partly because it nourishes the eye as the secundina uteri (chorion) do the fœtus.

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coat. Many authors include the first two portions under the designation chorioid.

Disregarding, then, this anterior portion, the middle coat presents two openings,—one anterior, the pupil, for the admission of the undulations of light; one posterior, the optic foramen of the chorioid, for the admission of the fibres of the optic nerve upon which those undulations take effect.

This envelope offers a striking contrast to the external one. While the latter is firm, dense, hard, and but scantily supplied with blood-vessels, the former is soft, easily torn, and extremely vascular. This is a natural consequence of its function, which is necessarily of a nutritive character; lying between the other two coats, it serves to nourish both. Again, while the outer coat is inextensible and immovable with respect to the others, the middle coat, being quite lax, can easily be stretched and moved. It is, therefore, a suitable seat for muscle-fibres which play an important part in the mechanism of vision. In color, too, the contrast is marked. The outer coat is either white or transparent; the middle one is a dark reddish brown in the posterior portion and of various opaque shades anteriorly.

Intra-ocular tension is doubtless kept up by the transudation of fluid from the vessels of the middle coat, which, viewed in this light, form a secreting organ of the very simplest form. Were it not for this provision, the fluids of the eye would rapidly decrease by filtration through the coats.

While this coat contains nerves in great abundance, they are for the most part not distributed within it, but pass to structures beyond. Inflammation here does not usually cause pain, unless its products distend the eyeball and occasion pressure.

THE CHORIOID.[1]

Considered in its most restricted sense, this portion of the middle coat extends from the nerve-entrance to the ora serrata,—that is to say, to about seven millimetres from the edge of the cornea. It therefore covers about the posterior two-thirds of the bulb. Its thickness varies from 0.1 millimetre near the nerve to 0.06 millimetre near the ora serrata.[2] Though

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[1] Syn.: *tunica chorioidea* or *choroidea*; *chorioidea* or *choroidea*; chorioid or choroid coat; choroid.

From *χόριον*, the chorion, + *εἶδος*, appearance, alluding to its vascular character, like that of the fœtal chorion.

The spelling *chorioid* is, for etymological reasons, to be preferred, although *χοροειδὴς* appears in some of the Greek authors. (Hyrtl.)

[2] The following statements as to the thickness of the chorioid are given by different authors:

	Near Nerve. Millimetre.	Near Ora Serrata. Millimetre.
Merkel	0.1	0.06
Sappey	0.4	0.3
Schwalbe, Gerlach	.05–.08	
Vierordt	.02	0.14–0.02

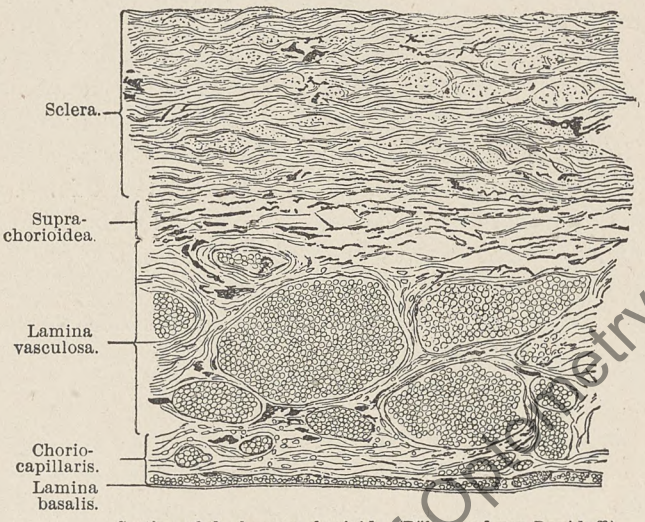
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closely applied to the sclera, it may be stripped from it, owing to the laxity of its external layer. It adheres more closely at the optic-nerve entrance than elsewhere, owing to the connective-tissue bundles and vessels that here pass from the chorioid to the nerve. The laxity of the membrane enables it to adjust itself to the variations in volume that occur in its very numerous blood-vessels.

Like the inner surface of the sclera, the outer surface of the chorioid is rough and fluffy from the loose ends of connective-tissue bundles severed by the separation of the two membranes. The inner surface is, however, smooth and easily separated from the outer or pigmented layer of the retina.

The color of the chorioid and also of the retina fades somewhat with advancing age, so that the pupil of the eye is less dark in old people. The

FIG. 34.



Section of the human chorioid. (Böhm and von Davidoff.)

color depends not only upon the pigment with which its cells abound, but also upon the copious supply of blood it contains.

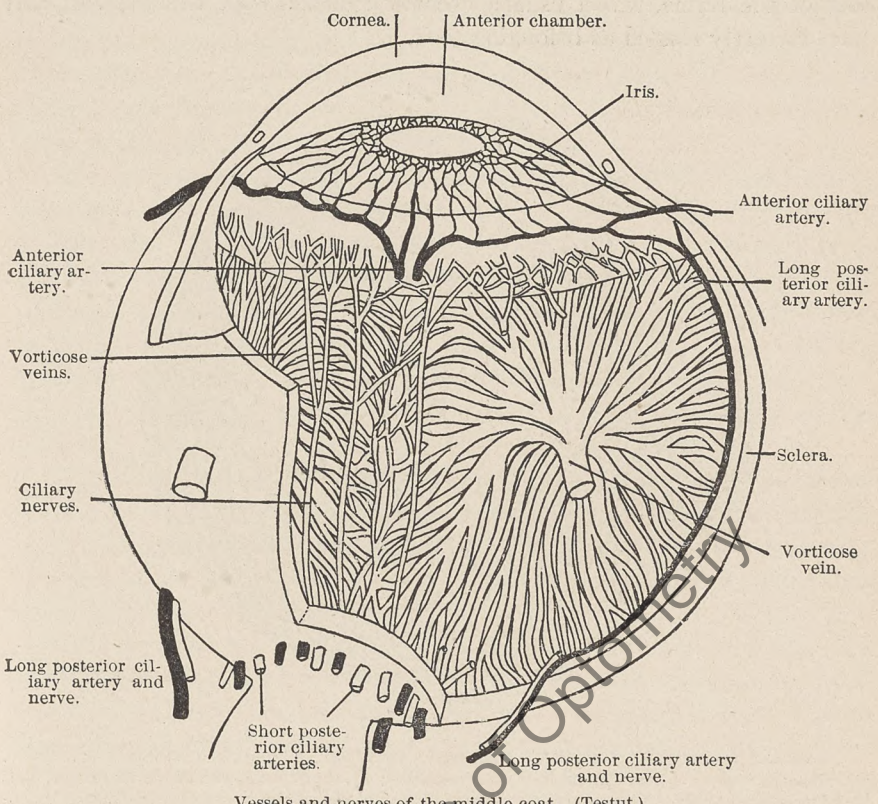
Its general appearance is that of a striated surface, the striations being caused by numerous vessels and nerves that pass from behind forward. These structures are united only by a thin web of connective tissue; hence the consistence of the chorioid is slight, resembling that of its homologue, the pia mater of the brain.

The essential characteristic of the chorioid is its vascular structure, and its different layers may be classified according to the predominant vessels each contains. This will be clearly seen by an inspection of Fig. 34. The principal layer, the lamina vasculosa, is almost wholly composed of large arteries and veins, and interior to this is the chorio-capillaris, made up of capillaries. These, the essential features of the chorioid, are separated from the adjacent coats of the eye by non-vascular layers,—on the outer surface

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the suprachorioidea, on the inner the lamina basalis. Some authors divide the outer portion of the vascular layer into two laminæ, one of larger vessels, the other (Sattler's layer) of smaller or medium-sized ones. This appears to be an unnecessary refinement, but it emphasizes the fact that in the chorioid alone, of all regions of the body, is seen a distinct gradation in size of vessels in superimposed layers. The reason for this is that the tissues requiring most active nourishment lie to the inner side. The sclera

FIG. 35



Vessels and nerves of the middle coat. (Testut.)

is comparatively inert and needs but little blood, while the retina is very active and requires a great supply. The nutrient fluids exude from the capillaries; hence these are developed on the retinal surface. This arrangement of the vessels explains why inflammatory exudations from the chorioid usually seek the inner surface, and are therefore so destructive in their effects.

The *suprachorioidea*[1] is essentially a continuation of the lamina fusca

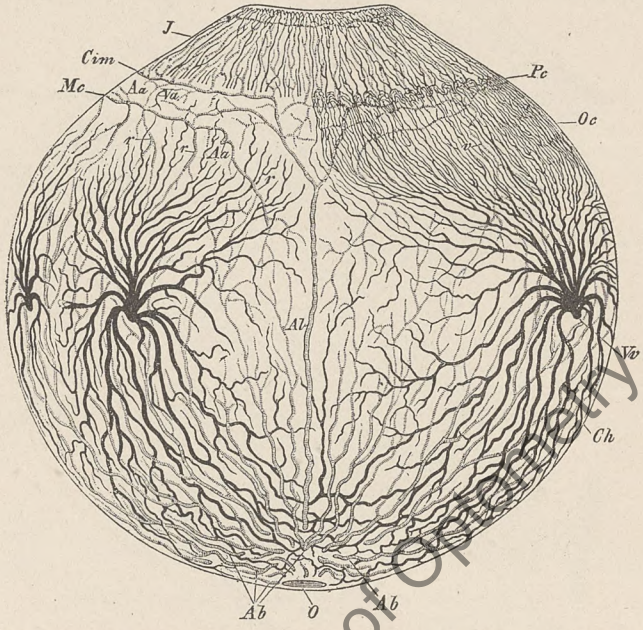
[1] Syn.: suprachorioidal lamina; *lamina suprachorioidea* or *suprachoroidea; membrana suprachoroidea* (Montain); ectochoroidea (Leidy); *tunica suprachorioidea* or *suprachoroidea; t. cellulosa; t. arachnoidea; membrana villoso-glandulosa.*

The last name was given by B. A. Stier, one of the earliest to describe this membrane, in a treatise "De tunica quadam oculi novissime detecta," Halle, 1759, from its villous appearance and certain glandular-like corpuscles which he thought he had discovered in it.

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of the sclera, from which it is separated when the sclera is torn away, cleavage occurring between the laminæ of connective tissue along the lines of the larger lymph-spaces, together constituting the perichorioidal space. Throughout the laminæ of this tissue numerous pigmented cells are found scattered, and these impart a characteristic reddish-brown hue to the membrane, which, when bathed in fluid and showing through the white web of the tissue, appears much like the inside of a grape-skin. These cells are stellate in form, and are to be distinguished from the pigmented, epithelial cells of the retina, which usually become detached with the chorioid, and were formerly classed as belonging to it.

FIG. 36.



Vessels of the chorioid. (Leber.)—*O*, optic-nerve entrance; *Ch*, chorioid; *Oc*, orbiculus ciliaris; *Pc*, ciliary processes; *J*, iris; *Aa*, anterior ciliary arteries; *Ab*, short posterier ciliary arteries; *Al*, long posterior ciliary artery; *Cim*, greater arterial circle; *Mc*, arteries of ciliary muscle; *rr*, recurrent arteries; *Vv*, vorticose veins; *Va*, anterior ciliary veins.

While the suprachorioidea has no vessels or nerves that specially belong to it, nevertheless it serves as the passage-way for many of these structures that pass from behind, near the optic-nerve entrance, forward to the ciliary body, the iris, and the cornea. (See Fig. 35.) The long ciliary arteries, two in number, penetrate the sclera almost exactly in the horizontal meridian, and, accompanied by two of the largest ciliary nerves, pass directly through the suprachorioidea. The external is slightly above, the internal slightly below, the horizontal meridian, and their situation should be remembered in operating upon the sclera. Exudations between the sclera and the chorioid may, it is said, by pressure on the nerves, cause changes in the pupil, though the iris is not otherwise involved. (Hyrtl.)

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The *lamina vasculosa*,[1] which succeeds the suprachorioidea, is a continuation of the connective-tissue web of the latter, with the addition of a great number of large vessels. The tissue is not laminated, but veins predominate in the more superficial portion, especially in front, the arteries lying somewhat deeper. Stellate pigment-cells also occur here.

The principal arteries are the short posterior ciliary, about twenty small branches derived from two trunks that arise from the ophthalmic artery above the optic nerve. These penetrate the sclera in the vicinity of the nerve-entrance (Figs. 35 and 36) and form a very rich net-work that is lost in the chorio-capillaris. Recurrent branches from the long posterior ciliary (Fig. 36, *oo*) and from the anterior ciliary trunks also supply the anterior part of the chorioid, the main distribution of these arteries being to the ciliary muscle and to the iris.

The removal of blood from the chorioid is almost wholly effected by four large vessels, called the vorticose veins,[2] that discharge into the ophthalmic vein. (Fig. 35; Fig. 36, *hh*.) This name is given them because they are formed of a large number of trunks that converge in long, sweeping curves to form a single one, the arrangement resembling a vortex or whorl. Those of the branches that come from the chorio-capillaris primarily arise from a sinus, towards which the capillaries converge, forming a minute vortex not wholly dissimilar to that of the larger trunks. (Fig. 37.)

The vorticose veins are usually grouped in two pairs, in each of which the vessels are symmetrically disposed on either side the vertical meridian nearly 90° apart. Those of the superior pair penetrate the sclera at seven to eight millimetres behind the equator, those of the inferior pair a little farther forward. Their course through the sclera is very oblique from without inward, and they also diverge from the vertical meridian, the passage occupying from two to four millimetres. From this oblique course it follows that they are particularly exposed to compression from without. Fuchs,[3] to whom we owe the most thorough investigation of the course of

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[1] Syn.: chorioid proper, *chorioidea propria; tunica vasculosa Halleri; stroma chorioidea;* mesochoroidea (Leidy).

[2] Syn.: *ductus oculi abducentes* (Hovius, 1716); *venæ* or *vasæ vorticosæ* or *verticosæ; venæ ciliares posticæ; Wirbel-* or *Wirbelvenen*, G.

Nicolaus Stenon, one of the earliest investigators into the vascular system of the chorioid, recognized the venous character of these vessels in his work "De musculis et glandulis observationum specimen," Hafniæ, 1664. Hovius also, in his "Tractatus de circulari humorum motu in oculis," Lugdunum Batav., 1716, considered them as veins, as will be seen by the name cited above. Frederic Ruysch, however, in an "Epistola de oculorum tunicis," 1721, described them as arteries, admitting two layers of arterial vessels in the chorioid,—viz., the lamina vasculosa, containing "ramusculi disposita in orbem," and the chorio-capillaris, to which his son Henry Ruysch gave the name of membrana Ruyschiana "in patris honorem." It was not until the time of Haller that this error was corrected.

[3] Fuchs (Ernst). Beiträge zur normalen Anatomie des Augapfels. Archiv für Ophthalmologie, 1884.

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these veins, thinks that at or near their exit they may be compressed by the action of the oblique muscles, the most favorable attitude for compression being that in which the eye is adjusted for near work. He suggests that such compression might, if long continued and habitual, cause, in young people whose tissues are yet plastic, a distention of the coats of the eye resulting in an elongation of the axis and consequent myopia.

Blood passes to the vorticose veins from all parts of the eyeball, branches converging from behind near the optic-nerve entrance and from the front about the ciliary body and the iris. Those that pass backward through the orbiculus ciliaris are for the most part straight, and give to this region its characteristic radiate appearance. All the intra-ocular veins are destitute of valves. Variations in the vorticose veins are not infrequent. These usually consist in an increase in their number caused by a doubling of one or more of their trunks. This occurs more frequently on the nasal side.

Bundles of delicate, non-striated, muscular fibres are found scattered throughout the chorioid.

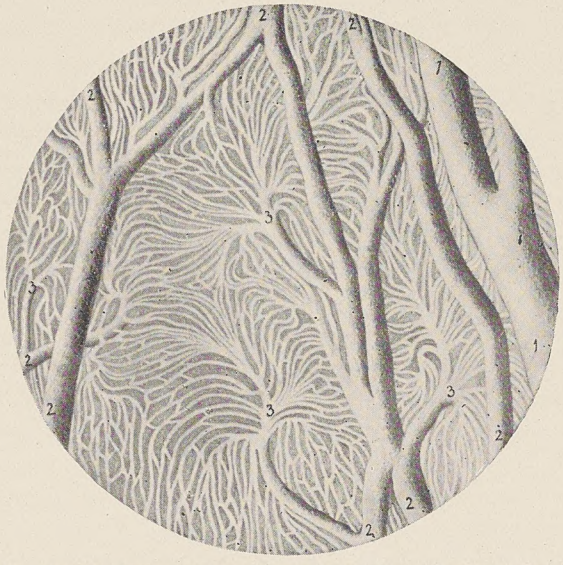
Sattler has described in the deeper portion of the lamina vasculosa a fine net-work of elastic fibres invested by a layer of endothelial cells. This he believes to be a vestige of the *tapetum*, a specialized layer of the chorioid found in some animals. Two kinds of this structure are described,—one, the *tapetum fibrosum*, found more especially in ruminants and pachyderms, formed of connective-tissue fibres; the other, the *tapetum cellulosum*, found in carnivora, made up of endothelial cells. The pigment of the retina being wanting over certain definite areas, light falls upon this opaque layer and is totally reflected at certain angles, causing a lustrous iridescence that gives rise to the popular belief that the eyes of animals may "shine in the dark." The iridescence is caused by slight irregularities of the reflecting surface, being an "interference phenomenon" like that seen in mother of pearl.

The vascular net-work of the *chorio-capillaris*[1] (Fig. 38) is extraordinarily rich. The vessels show a remarkable uniformity of calibre, averaging about 9 μ in diameter, and the meshes of their net-work are very close, being 10–20 μ behind, near the macula lutea, 15–30 μ at the equator, and 25–30 μ near the ora serrata. This is the most copious capillary net-work of the body, even surpassing that of the alveoli of the lungs. The necessity for this copious supply of blood is apparent when we find that the most active part of the retina, the rod and cone layer, has no vessels of its own, but is dependent upon this net-work for its nutrition. The reddish color of this layer shows through the retina, and is a striking characteristic of the interior of the eye when the latter is viewed through the ophthalmoscope.

[1] Syn.: *membrana chorio-capillaris*; *lamina Ruyschii* or *tunica Ruyschiana* (for Frederic Ruysch, professor of anatomy at Amsterdam, 1638–1731); *membrana Hovii* (for Jacobus Hovius, a Dutch physician, known by his "Dissertatio de circulari humorum oculorum motu," published in 1716 at Leyden. Appears to be prior); entochoroidea (Leidy).

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FIG. 37.



The origin of the chorioidal veins. (Arnold.)—1, 1, one of the larger veins; 2, 2, communicating veins; 3, 3, "stars of Winslow," or vortical whorls of capillaries by which the latter arise from the chorio-capillaris.

FIG. 38.



The chorio-capillaris × 100. (Sappey.)—1, 2, 3, veins of the lamina vasculosa; 4, a similar vein arising from the chorio-capillaris by convergent branches; 5, 5, the capillary net-work formed by the anastomosis of similar convergent systems.

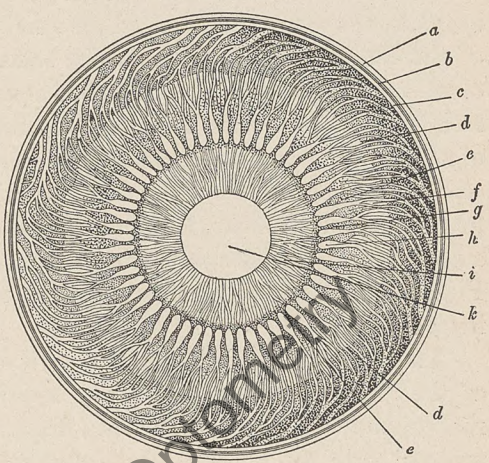
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It is in this layer that are found the capillary whorls, already mentioned, that form the beginning of the vorticose veins. (See Fig. 37.) These are known as the *stars of Winslow*,[1] and are not dissimilar to the stars of Verheyen found under the capsule of the kidney. They are not as well marked in man as in animals that possess a tapetum. No pigment, no great vessels, and no nerves are found in this layer.

The *lamina basalis*[2] appears to be merely a condensation of the connective-tissue stroma of the preceding layers, like the basement membrane of epithelium. It is thin, clear, and transparent, structureless or showing faint fibrillation on the vascular side, being firmly united to the chorio-capillaris, from which it can be separated only by maceration with strong alkalies or acids. When so treated, it comes away in shreds that have a tendency to roll up as does the limiting layer of the cornea. With age it increases in thickness, and sometimes produces hemispherical elevations that press upon the retinal pigment and destroy it. (H. Müller.)

FIG. 39.



The ciliary body seen from behind.—*a*, sclera; *b*, chorioid; *c*, retina; *d*, *d*, ora serrata; *e*, *e*, the ciliary body, divisible into *f*, the orbiculus ciliaris, a ring of radiating filaments, and *g*, the corona radiata, composed of a ring of ciliary processes, *h*; *i*, iris; *k*, pupil.

THE CILIARY BODY.

On looking at the anterior half of an eye bisected at its equator, there can be seen on the inner surface of its coats, about seven millimetres from the iris, a delicate, wavy line forming a ring. This is the *ora serrata* (Fig. 39, *d*, *d*), already mentioned, and marks the boundary of the nervous elements of the retina as well as that of the chorio-capillaris by which those elements are fed. In front of this line the inner surface is marked with delicate striations resembling fine hairs or cilia,[3] especially well marked anteriorly, due to delicate vessels meridionally arranged, and to slight folds of the surface. These were noted by the older anatomists, being mentioned by Galen, who

[1] *Stellulæ vasculosæ Winslowii* (for Jacques Bénigne Winslow, a physician of Paris, 1669–1760).

[2] Syn.: *membrana pigmenti* (Bruch, Zur Kenntniss des körnigen Pigments, Zürich, 1844. He believed it to be composed of delicate young epithelial cells, from which the pigment cells of the retina are developed); *membrana Bruchii;* Bruch's layer; *m. intrachorioidea* (Luschka, who, however, includes with it under this designation the pigmented layer of the retina); *lamina basilaris; l. elastica chorioidea* (Kölliker); *l. vitrea chorioidea* (Arnold); vitreous or hyaline layer or membrane.

[3] Filaments of Ammon. (Wallace)

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considered that they were intended partly for the conveyance of nutriment to the lens, and partly for uniting the chorioid with the iris and cornea. Vesalius[1] described them in similar terms, and from his description this part of the eye became known as the *ciliary region*, and the portion of the middle coat here situated as the *ciliary body*.[2]

Extending from the ora serrata to the attached border of the iris, it is from six to seven millimetres broad. It is divided into two zones,—a comparatively smooth, posterior one, the *orbiculus ciliaris* (Fig. 39, *f*), showing merely the slight striations already mentioned, and a plicated anterior one, the *corona radiata* (Fig. 39, *g*), much thickened by a number of folds or elevations, the *ciliary processes*, arranged meridionally, encircling the detached border of the iris just back of the corneo-scleral junction. It is thickened by the interposition between it and the sclera of a zonular band of non-striated muscle-fibres forming the *ciliary muscle*.

The *orbiculus ciliaris*[3] (Fig. 40, *h*; Fig. 39, *f*) is about four millimetres broad, and is distinguished from the chorioid proper not only by the absence of the chorio-capillaris, but also by some changes in the connective-tissue elements. The vessels are all about equal in calibre, and run parallel to each other without branching. The connective tissue that unites the vessels of the lamina vasculosa again appears here, but in reduced quantity. The elastic layer of Sattler is, on the contrary, somewhat increased. Losing its endothelial elements, it extends upon the inner surface of the vessels as a reticulum. The lamina basilaris is continued forward without change. Pigment from the pigmented layer of the retina usually adheres to the inner surface.

The *corona radiata*[4] (Fig. 39, *g*) is composed of about seventy folds of the inner surface of the ciliary body, arranged like a fluted collar or ruff around the edge of the iris. Each of these folds is termed a ciliary process[5] (Fig. 39, *h*; Fig. 40, *d*), and it is these that have given the name to the entire region.

---

[1] "Verum hæc tunica tenuitate aranearum telas fere superat; et processulis ab uvea pronatis talibus constat, ut nigra cilia, seu palpebrarum pilos forma insigniter exprimat." Vesalius, De corpore humani fabrica, 1543, lib. vii. cap. xiv. p. 648.

[2] From L. *ciliaris*, adjective from *cilium*, an eyelash or fine hair. "Dicunt autem ciliarem, quia ciliis non absimilis est." Casserius, Pentæsthesion, cap. xxvi. p. 286.

Syn.: *tunica ciliaris* (Vesalius); *corpus ciliare* (Fallopius); *ligamentum ciliare*; *l. sclerotico-chorioidale* (von Ammon); *circulus* or *annulus ciliaris*; *orbiculus ligamentosus* (Krause); *Strahlenband*, G.; *zone choroïdienne* (Sappey); *zone ciliaire* (Testut). Those terms which imply a ligament refer more particularly to the external, whitish portion of the ciliary body. Krause calls the deeper, soft layer the *orbiculus gangliosus*.

Henle, Gerlach, and some other modern authors apply the term *corpus ciliare* to the corona radiata + the ciliary muscle.

[3] Syn.: *pars non plicata*; *p. striata* (Zinn).

[4] From L. *corona*, a crown or garland, and *radiata*, surrounding like a halo.

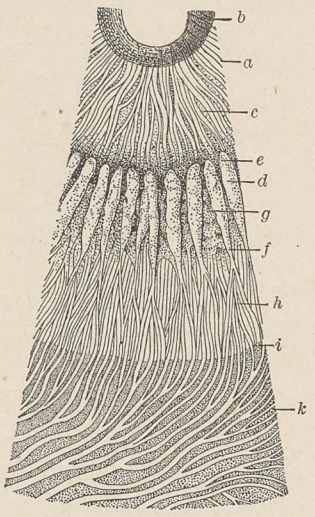
Syn.: *pars plicata*; *Strahlen-* or *Faltenkranz*, G.; *corpus ciliare* in the restricted sense; the ciliary processes.

[5] Syn.: *processus ciliaris* (Th. Bartholin, 1655); *plica ciliaris*; *ligamentum ciliare*.

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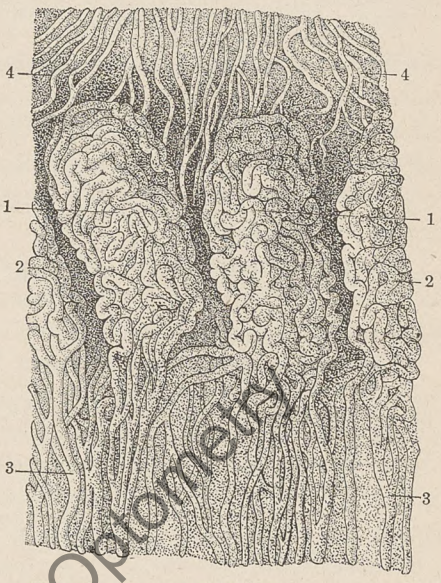
The slight striations of the orbiculus ciliaris are so arranged that three or four of them unite to form a ciliary process. Like those striations, the processes are of a vascular character, each being composed of a skein-like glomerulus of vessels (Fig. 41) covered with a thickened continuation of the basement layer. Although of different shape, their structure recalls that of the glomeruli of the kidney, and it is probable that the analogy also holds good in respect to their offices, both allowing fluids from the blood which they contain to escape through their walls. It is thought that they are the principal agents in the secretion of the aqueous humor. Certain recesses in the surface of the processes resemble very much, on section,

FIG. 40.



Segment of the ciliary body and of the iris. (Sappey.)—*a*, iris; *b*, its pupillary zone; *c*, its ciliary zone; *d*, a ciliary process; *e*, its apex; *f*, its base; *g*, ciliary folds; *h*, striations forming the orbiculus ciliaris; *i*, ora serrata; *k*, chorioid with its vessels.

FIG. 41.



Vascular plexuses of the ciliary processes. (Sappey.)—1, 1, two ciliary processes formed by anastomosing veins; 2, 2, portions of two others; 3, 3, venules passing from the processes to the vasa vorticosa; 4, 4, veins from the iris discharging into the ciliary processes.

the lumen of glands, and have accordingly been named by Collins[1] the *ciliary glands*.

The arteries of the processes are derived from the long posterior ciliary through a plexus formed by those vessels about the iris (greater arterial circle). After several subdivisions they pass into a set of very large convoluted capillaries, and thence into veins that run parallel through the orbiculus ciliaris to empty into the vorticose veins.

The size of the processes is somewhat variable, they being from two to

[1] Collins (E. T.). The Glands of the Ciliary Body in the Human Eye. Tr. Oph. Soc. U. Kingdom, Lond., 1890–91.

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three millimetres in length, 0.12 millimetre in breadth, and from 0.8 to one millimetre in height. Between the longer ones smaller plications may be seen, the *ciliary folds*[1] (Fig. 40, *g*), which appear to be simple continuations of the striæ of the orbicularis.

The most elevated portion of the processes is a little in front of the margin of the lens and at a distance of 0.5 millimetre from it, so that it is possible to see the iris from behind through the interval. The anterior end forms, therefore, a portion of the wall of the posterior chamber. The zonula ciliaris, which is a specialized portion of the membrane enclosing the vitreous humor, extends over the posterior portion of the corona radiata, being applied closely to the processes and descending into all the interstices between them. A well-marked furrow separates the corona from the iris.

The numerous vessels of the corona are united by a delicate stroma of fibrous connective tissue, within which are scattered numerous pigment-cells. This is thickened on its inner surface to a basement membrane, to which there usually adheres the dark pigmented layer of the retina. In preparing the inner coat for examination, this is frequently brushed away from the ciliary processes, which then appear grayish white upon an intensely black ground.

The great vascularity of this region makes it very subject to inflammation when interfered with. It is, therefore, avoided as much as possible in all operations upon the eye.

The *ciliary muscle*[2] has a curious history. It was early thought that muscular fibres must exist in this region of the eye, and Eustachius[3] actually figures the ciliary body as a muscle, giving it, in fact, the name *musculus ciliaris*. This seems, however, not to have been generally known at the time, owing to the loss of his plates, Vesalius and Fallopius not mentioning it. Kepler,[4] the astronomer, in his consideration of the optical properties of the eye, was led to suppose that muscular fibres existed in the region about the lens, by which it was moved backward and forward to adapt it to vision at different distances. Scheiner[5] also attributed to the ciliary processes a faculty of movement by which they could affect the lens. Plempius[6] supposed muscular fibres to exist there which drew the

[1] Syn.: *plicæ ciliares* (C. Krause).

[2] Syn.: *musculus ciliaris* (Eustachius); *ligamentum ciliare* (Fallopius); *annulus ciliaris* (Luschka); *tensor choroidea* (Brücke); *musculus Brueckianus* (Donders); *ganglion ciliare* (Bochdalek); Brucke's muscle; Bowman's muscle.

[3] In Fig. VI., Plate XL., of the beautiful plates of Eustachius there is a good representation of an eye dissected so as to show the ciliary processes, with the following description: [Figura VI., patefacit] "... pupillam cum crystallino humore, et ligamento seu musculo ciliare." These plates were prepared by Eustachius from 1552 to 1574, lost, found by Pope Clement XI., and first published by his physician Lancisi in 1714. The text accompanying the plates has never been recovered.

[4] Kepler (Johannes). Dioptrice. Augustæ Vindelicorum [Augsburg], 1611.

[5] Scheiner (Christopher). Oculus. Œniponti [Innspruck], 1619, pp. 162, 163

[6] Plempius (Vopiscus Fortunatus). Ophthalmographia. Amstelodami [Amsterdam], 1632, p. 169.

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retina forward. Descartes[1] appears to have first suggested that such fibres altered the form of the lens, in which he was followed by Briggs.[2] Many other anatomists[3] surmised the existence of this muscle, but the first to demonstrate it microscopically appears to have been William Clay Wallace,[4] of New York, who revived Eustachius's name, ciliary muscle. Brücke[5]

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[1] Descartes (Réné). La dioptrique. Leyden, 1637, cap. iii.–v.

The same. L'Homme. Paris, 1664.

[2] Briggs (William). Ophthalmographia. Lugd. Batav. [Leyden], 1686.

[3] The following may be mentioned among others:

Vesling (J.). Syntagma anatomica. Amstelodami, 1647.

Bartholin (Thomas). Anatomia. Hagæ-Comitiis [The Hague], 1663.

Willis (Thomas). De anima brutorum. Genevæ, 1676.

Sturm (J. C.). Oculus: de visionis organo et ratione genuina dissertatio. Altdorffi, 1678, p. 13.

Zahn (R. P. F. J.). Oculus artificialis teledioptricus. Herbipoli [Würzburg], 1685, p. 15.

Bidloo (Godberi). Anatomia humani corporis. Amstelodami, 1685.

The same. Observationes de oculis et visu variorum animalium. Lugd. Batav., 1715.

Wedel (Christ.). Epistola ad Fr. Ruysch, de oculorum tunicis. Amstelodami, 1700.

Keill (James). The Anatomy of the Humane Body. London, 1703, p. 160.

Walther (Aug. F.). De lente crystallina oculi humani. Lipsiæ [Leipsic], 1712.

Morgagni (J. B.). Epistolæ anatomicæ. 1728.

Porterfield (William). An Essay concerning the Motions of our Eyes. Med. Essays and Obs. Soc. Edinb., 1735, iii. 160; 1737, iv. 124.

The same. A Treatise on the Eye. Edinburgh, 1759.

Ruysch (Fred.). Responsio ad Wedelium de oculorum tunicis. 1737.

Platner (J. Z.). De motu ligamenti ciliaris. Lipsiæ, 1738.

Boerhaave (H.). Prælectiones academicæ, edit. et not. add. Alb. Haller. Taurini [Turin], 1742–45.

Camper (P.). De quibusdam oculi partibus. Lugd. Batav., 1746.

Olbers (H. W. M.). De oculi mutationibus internis. Gottingæ, 1780.

Hildebrandt (G. F.). Anatomie des Menschen. 1803.

Graefe (K. A.). Ueber die Bestimmung der Morgagnischer Feuchtigkeit, der Linsenkapsel und des Faltenkranzes. Archiv f. d. Physiologie, Halle, 1809, ix. 225–336.

Brewster (D.). Experiments on the Structure and Refractive Power of the Coats and Humors of the Human Eye. Edin. Phil. Jour., 1819, i. 42–45.

Jacobson. Suppl. ad Ophthalm. Copenhagen, 1821.

Purkinje (J. E.). Beobachtungen und Versuche zur Physiologie der Sinne. Berlin, 1825.

Müller (J.). Zur vergleichenden Physiologie des Gesichtsinns. Leipzig, 1826, p. 172.

Smith (Thomas). On the Muscular Structure and Functions of the Capsule of the Crystalline Lens and Ciliary Zone. Lond. and Edinb. Phil. Mag., 1833, 3d ser., iii. 5.

[4] Wallace (William Clay). On the Accommodation of the Eye to Distances. American Journal of Sciences and Arts, 1835, xxvii. 219–222.

In this article he says, "At the base of the ciliary processes upon the inner surface of the chorioid coat there is a range of muscular fibres. In the sheep the fibres of the upper portion run transversely to the ciliary processes; those of the lower portion run parallel to them."

See also the following by the same author: Treatise on the Eye, New York, 1839, p. 37. Lond. Med. Gaz., 1842–43, i. 412. Lectures on Myopia, Boston Med. and Surg. Jour., 1844, xxx. 289, 290. Accommodation of the Eye to Distances, New York, 1850.

[5] Brücke (Ernst). Ein neuer Muskel im Auge. Med. Zeitung, Berlin, 1846, xv. 130.

The same. Ueber den Musculus Cramptonianus und den Spannmuskel der Choroidea. Müller's Archiv, 1846, p. 370. (Vorgetragen in der Berliner physikalischen Gesellschaft am 29 Mai, 1846.)

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published a description of the muscle in 1846, and its discovery is often wrongly ascribed to him. Bowman[1] gave an excellent account of it one year later, also calling it by its present name, which is frequently credited to him. Even this is not all. The deeper circular fibres were first mentioned by Wallace, afterwards described and figured by Van Reeken,[2] and described by Rouget;[3] yet, since somewhat later they were described by H. Müller,[4] the honor of their discovery is usually allowed him.

The muscle in question is a zone-like band of smooth fibres interposed between the ciliary body and the sclera, and may perhaps be regarded as a condensation of the scattered bundles of smooth muscle-fibres found elsewhere in the middle coat. Its grayish appearance caused it to be long regarded as a ligament. It occupies a zone from six to seven millimetres wide, taking its origin from the thickened band already described as the annular ligament, quickly expanding to a maximum thickness of 0.8 millimetre, and then gradually thinning away to an insertion upon the chorioid, the muscular fibres blending with the stroma and passing as they disappear into some peculiar stellate figures. (Iwanoff.) It extends a little farther on the temporal side than on the nasal, and H. Müller describes bundles that accompany the long ciliary arteries as far as their scleral canals. A meridional section of the muscle is, therefore, triangular, the longest sides of the triangle being applied to the sclera and to the ciliary body, a short base being directed towards the iris.

Two principal divisions of the muscle may be made out, corresponding to the direction of its fibres. First, an external condensed portion, in which the fibres run meridionally; this was the portion which was first noted by Brücke, and which he called the *tensor chorioideæ*. Second, an internal

[1] Bowman (William). Lectures on the Parts concerned in the Operations of the Eye, and on the Structure of the Retina, delivered at the Royal London Ophthalmic Hospital, Moorfields, June, 1847.

[2] Van Reeken (C. G.). Ontleedkundig onderzoek van den toestel voor accommodatie van het oog. Utrecht, 1855.

[3] Rouget (Charles). Recherches anatomiques et physiologiques sur les appareils érectiles: Appareil de l'adaptation de l'œil chez les oiseaux, les principaux mammifères et l'homme. Compte-rendu de l'Acad. des Sciences, Paris, 19 Mai, 1856, xlii. 937.

The same. Sur la structure de l'œil et en particulier sur l'appareil irio-choroïdien. Compte-rendu de la Soc. de Biologie, Gaz. méd. de Paris, 1856, 3e sér., xi. 563.

The same. Réponse à une réclamation de priorité adressée par M. Müller. Comptes-rendus de l'Acad. des Sciences, Paris, xlii. 1255–1256.

[4] Müller (H.). Sitzungsberichte der physikalisch-medicinischen Gesellschaft in Würzburg, Sitzung vom 24. November, 1855. Verhandl. d. phys.-med. Gesellsch. in Würzb., 1856, vi. 26.

As this is the passage upon which Müller rests his claims to priority, it is given entire for comparison with Wallace's notice:

"Hr. H. Müller theilt eine Notiz über eine ringförmige Schicht im Ciliarmuskel des Menschen mit. Dieselbe liegt, bedeckt von dem Langsbündeln des Muskels, auf dem vordersten Theil des Ciliarkörpers und Hr. Müller glaubt dass sie für die Accommodation des Auges von besonderer Wichtigkeit sei."

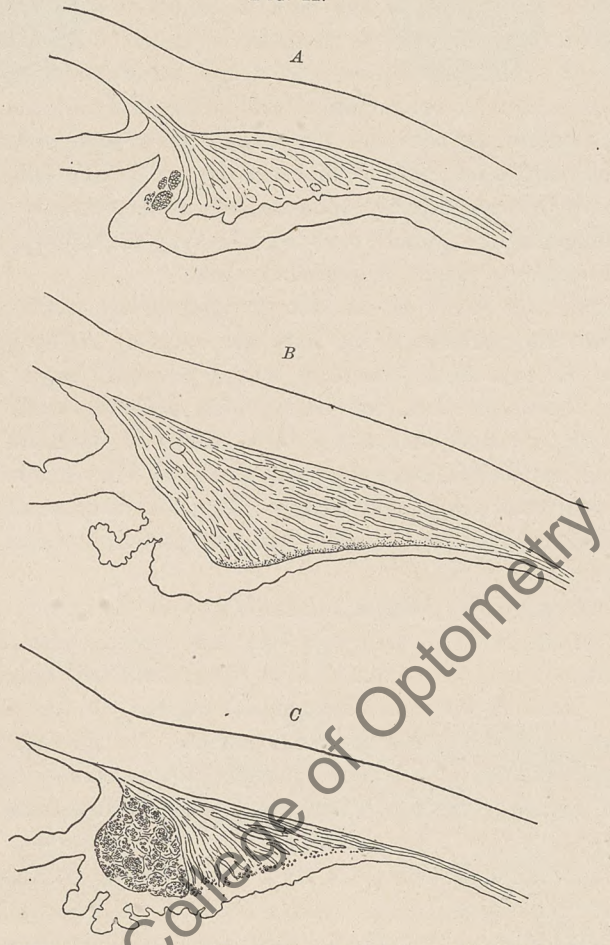
The same. Ueber ein ringförmigen Muskel am Ciliarkörper des Menschen und über den Mechanismus der Accommodation. Arch. f. Ophth., Berl., 1857, iii., 1 Abth., 1–24.

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portion that surrounds the margin of the iris, with fibres running in an equatorial direction; this is the *compressor lentis*[1] of H. Müller, and constitutes about one-tenth of the entire muscle. Its outer fibres have looped connections with other portions of the muscle.

Besides these clearly defined portions, other subdivisions have been suggested. Iwanoff[2] describes the deeper part of the tensor chorioideæ,

FIG. 42.



Varieties of the ciliary muscle. (Iwanoff.)—*A*, form found in emmetropic eyes; *B*, in myopic eyes; *C*, in hypermetropic eyes.

which is arranged in a loose, reticulate manner, as the *radial* portion. Waldeyer[3] found in some eyes a bundle passing from the annular ligament to the sclera, where in birds is situated a well-marked band of striated muscular fibres, the Cramptonian muscle. This has not been observed by

[1] Syn.: Müller's muscle.
[2] Stricker's Manual of Histology, Am. ed., p. 851.
[3] Gräfe und Sämisch, Handbuch, i. 231.

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others, so far as I am aware, and it seems doubtful if structures of such distant phylogenetic relation are truly homologous.

Well-marked variations of the muscle occur. Iwanoff has pointed out that in myopic eyes the circular fibres are deficient or entirely absent, while in hypermetropic eyes they are greatly increased, so as to cause a decided enlargement of the ciliary body, and they then amount to at least one-third of the entire mass of the muscle. (See Fig. 42.)

The action of the muscle has been a subject of some discussion. It was early observed that the eye possesses a power of adjustment for the vision of near or remote objects, and it was naturally thought that this result, which is called *accommodation*, was produced by an alteration of the relative positions of the lens and the retina. Most early observers of the ciliary muscle supposed that its function was to produce an effect of this kind either by drawing directly upon the lens or the retina by compressing and thus elongating the eyeball, or by compressing the anterior ciliary veins, which, thus rendered turgid, displaced the lens.

The matter was finally set at rest by observations made upon images reflected from the surfaces of the lens and cornea. Although nearly all light passes through these structures, yet if a small, bright flame be so placed in a darkened room that its rays fall obliquely upon the eye, an observer on the opposite side can see three images of the flame reflected,—the first, erect and bright, from the outer surface of the cornea; the second, erect and somewhat larger and dimmer, from the anterior surface of the lens; the third, inverted and smaller, from the posterior surface of the lens. (See Fig. 43.)

These are called the images of Purkinje[1] or Sanson.[2] The second image may be observed to change in size and position when the vision is directed from a near object to one close at hand, while the other two remain stationary. This shows that the anterior surface of the lens changes during accommodation, while the other surfaces remain unaltered. The matter is rendered still more plain by using two sources of light, making two sets of images, one above and one below the horizontal meridian. (See Fig. 44.)

The first to notice the change of the images during accommodation appears to have been Langenbeck,[3] but his observations were imperfect. In 1851 both Cramer[4] and Helmholtz[5] improved upon his experiments and

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[1] Purkinje (J. E.). De examine physiologico organi visus et systematis cutanei. Vratislaviæ [Breslau], 1823, p. 28.

[2] Sanson (L. J.). Leçons sur les maladies des yeux. Paris, 1838.

[3] Langenbeck (Max). Klinische Beiträge aus dem Gebiete der Chirurgie und Ophthalmologie. Göttingen, 1849.

[4] Cramer (A.). Mededeelingen uit het gebied der ophthalmologie. Tijdschr. d. Nederl. Maatsch. t. Bevord. d. Geneesk., 1851, ii. 99: Nederl. Lancet, 1851, ser. 3, i. 529.

[5] Helmholtz (H.). Beschreibung eines Augenspiegels. Berlin, 1851.

The same. Ueber die Accommodation des Auges. Arch. f. Ophth., Berlin, i., Abth. ii. 1.

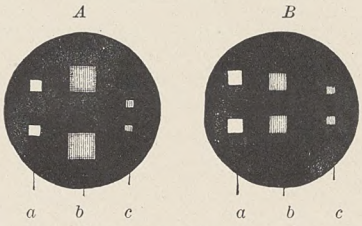
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FIG. 43.



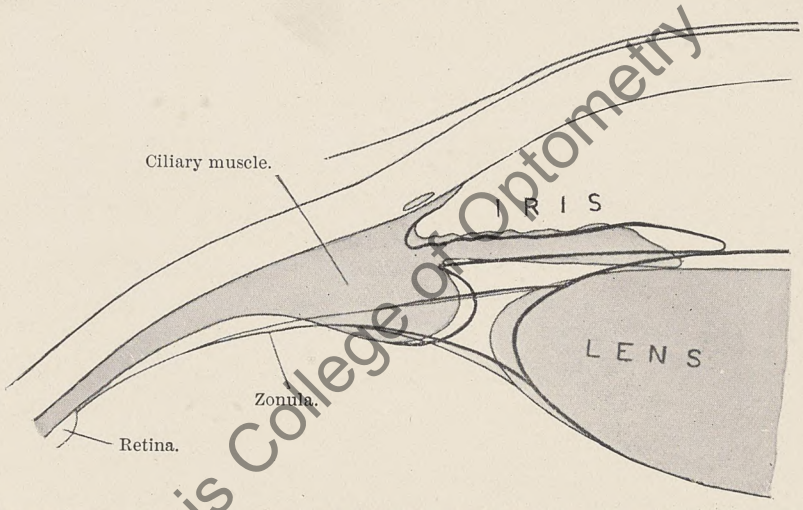
Images of Purkinje formed by reflections from the surfaces of the eye. (Helmholtz.)—*a*, reflection from the cornea; *b*, from the anterior surface of the lens; *c*, from the posterior surface of the lens.

FIG. 44.



Double images of Purkinje used for showing the curvature of the lens during accommodation. (Helmholtz.)—The small letters as in last illustration. *A*, appearance during accommodation for distant vision; *B*, for near vision.

FIG. 45.



Action of the ciliary muscle. (Fuchs.)—The shaded portion shows the parts when at rest, the heavy line their displacement when the ciliary muscle is in action.

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showed clearly the amount of curvature. Helmholtz, in particular, demonstrated that the anterior surface curved most, and, indeed, that the curvature can be seen by carefully observing any eye from the side while directed alternately to distant and near objects. The posterior surface curves but little, and the lens does not shift its position. Accommodation is effected by altering the curvature of its surfaces and thus changing its refractive power. The suspensory ligament of the lens, which will be hereafter described, is closely connected with the ciliary body and with the chorioid. The lens is held by it in a state of tension, and when this tension is relaxed tends to assume a spherical form. The ciliary muscle, having its *punctum fixum* at the unyielding corneo-scleral junction, has its *punctum mobile* upon the chorioid, which, as Brücke surmised, it draws forward. When this is done, the suspensory ligament is relaxed (see Fig. 45), the iris and the equator of the lens are pushed towards the axis of the eye, the surfaces of the latter are more curved and the anterior one is pushed towards the cornea. The circular fibres act more directly and effectively than the meridional ones; hence it is not surprising to find that in far-sighted persons, who have to accommodate a great deal (hypermetropes), the circular fibres are greatly developed, while in those who are near-sighted and accommodate but little (myopes) there is little or no development of those fibres.

The long and the short ciliary nerves supply the ciliary muscle. The former are derived from the nasal branch of the ophthalmic, and are, therefore, sensitive; the latter are from the ciliary ganglion, and are doubtless of a mixed character. They penetrate the sclera near the entrance of the optic nerve (see Fig. 35), run forward in the suprachorioidal space, enter the ciliary muscle, and there unite in a plexus (the ciliary plexus)[1] which contains scattered nerve-cells. From this plexus fibres are given off that pass to the cornea, the iris, and the ciliary muscle.

Arnstein and Agababow[2] have recently described the following nerve-endings in the ciliary body: 1, vaso-motor endings in the walls of the ciliary vessels; 2, motor endings in the ciliary muscle like those characteristic of smooth muscle-fibre elsewhere; 3, "reticular plates," or extremely fine reticulations of granular nerve-fibres; 4, terminal arborescences, or "telodendra," lying in the connective tissue between the bundles of muscle-fibres. The reticular plates probably minister to ordinary sensation, the arborescences to "muscular sense," being appropriately situated for irritation by the contraction of the muscle-bundles. This sense would be of great importance in an organ like the ciliary muscle, and admit of an accurate adjustment of accommodation.

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[1] Syn.: *plexus gangliosus ciliaris; orbiculus gangliosus ciliaris.* (W. Krause.)

[2] Die Innervation des Ciliarkörpers. Anatomischer Anzeiger, 1893, viii. 555.

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THE IRIS.[1]

This anterior section of the vascular coat is visible on looking into the eye through the transparent cornea, appearing as a thin, contractile, variously colored curtain, pierced with a central aperture, the pupil. Its peripheral or ciliary border is attached to the inner surface of the eyeball; its central or pupillary border is free, and rests upon the anterior capsule of the crystalline lens, which gives it firm support in its movements. It therefore divides the aqueous chamber into two lesser cavities, the anterior chamber between it and the cornea, and the posterior chamber between it and the lens.

It is sometimes stated that the iris lies in a vertical frontal plane, but a little examination shows that this is not strictly correct. As its pupillary border rests upon the lens, which projects beyond the plane of its ciliary border, its form is rather that of a very flat truncated cone placed with its outer rim vertical. When the lens is absent it may hang vertically, and then, losing its support, may tremble and shake with the movements of the ball.

The thickness of the iris is only 0.4 millimetre, decreasing somewhat towards the pupillary border. With wide dilatation of the pupil, or during inflammation, its thickness may be nearly doubled. Its total diameter is from ten to twelve millimetres, and when at rest its breadth from the ciliary border to the pupil is from four to five millimetres, a little less on the nasal side, the pupil being slightly eccentric. The diameter of the pupil is from three to six millimetres when the iris is at rest, but constantly varies, ranging from one to eight millimetres.[2]

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[1] From ἶρις, -ιδος, the rainbow or any bright-colored circumscribing circle.

Syn.: *tunica cœrulea; diaphragma bulbi; Regenbogenhaut*, G.; *Blendung*, G. (lit. *the screen* or *blind*).

Galen applies the term to the annular ligament (De usu partium, chap. ii.). Varolius and others of the older authors use it for the varied colors themselves. Scheiner calls the iris *sol*. Vesalius appears to have been aware of its duplex character, describing it as composed of two layers; and Jacobus Sylvius calls it *duplata meninx*.

[2] Different authorities vary slightly in their statements of these dimensions. The following are the principal ones given:

	Thickness of Iris.	Diameter of Iris.	Breadth of Iris Ring.	Diameter of Pupil.
	Millimetres.	Millimetres.	Millimetres.	Millimetres.
Quain	0.4	11	5	1–8
Testut	0.3	12–13	. .	. .
Sappey	. .	13	. .	3–4
Henle	0.4–0.2	. .	3.5–4.5	3–6
Rauber	0.4	10–12	4–5	3–6
Merkel	0.4–0.2	. .	4	4
Vierordt	0.4	11	. .	. .
Gerlach	0.3	9–10	. .	3–6
Schwalbe	0.4–0.2	. .	4–5	3–6
Krause	0.4	. .	. .	3–3
Chauvel and Nimier (Dict. encycl. d. sc. méd.)	. .	13	. .	3–4
Budge	. .	. .	. .	5.33–7
Huschke	. .	. .	. .	3.37–6.75

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According to Krause, the centres of the pupils are distant from each other 58.5 to 67.5 millimetres.

The weight of the iris is, according to Huschke, fifty-six milligrammes, being $\frac{1}{121}$ of that of the whole eye, and $\frac{1}{8}$ of that of the chorioid.

The attached or *ciliary border*[1] of the iris is continuous behind with the ciliary body, in front with the posterior limiting membrane of the cornea through the pectinate ligament. Its place of attachment is at the annular ligament, forming the inner boundary of the scleral sinus, as shown in Fig. 29. It coincides with the inner edge of the corneo-scleral bevel, and is, therefore, some three millimetres behind the apparent rim of the cornea as it appears externally. When it is desired to reach the lens without interfering with the iris, it is necessary to insert the instrument a little beyond this interval. The tissue of the iris is so loose that it is easily detached from its insertion. Hyrtl[2] mentions a case in which a complete separation of the iris was caused by a blow on the eye.

The free or *pupillary border*[3] is very thin, and, being of a clear black, owing to the pigment of the posterior surface that here turns over the border, cannot well be seen against the dark background of the pupil unless the posterior portion of the eye is removed. Examined through a glass, it presents a denticulate or beaded appearance, due to slight elevations formed at the junction of the striæ of the anterior surface, which will presently be described. That the plane of this border lies posteriorly to the plane of the anterior edge of the sclera can easily be demonstrated in the living subject by Helmholtz's experiment of viewing the eye from the side in such a position that the near edge of the sclera almost obscures the pupil. (See Fig. 46.) There is then apparent in front of the pupil a clear strip, due to a distorted image of the iris refracted by the cornea, and farther forward, directly against the convex edge of the cornea, a darker strip, which is the image of the opposite sclera. When the observer moves his eye farther back the first image disappears, but the second remains, which shows that the iris must lie behind the scleral rim. In viewing the iris in this manner it appears convex. It was accordingly described as of that shape by Galen, Vesalius, and many subsequent anatomists. This appearance is due, however, to a distortion of its figure by the passage of rays through the cornea and aqueous humor. When the eye is viewed under water—this having nearly the same index of refraction—it appears plane or nearly so.

The fact that the pupillary border touches the anterior surface of the lens can also be shown by direct observation with the figures of Purkinje, already referred to. (See Figs. 43 and 44.) It will be remembered that the second of these figures is that reflected from the anterior surface of the lens. The observer may easily take such a position that this reflection just touches the edge of the pupil, and if this position is slightly shifted back-

[1] Syn.: *margo ciliaris.*

[2] Topographische Anatomie, i. 245.

[3] Syn.: *margo pupillaris.*

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ward the image at once completely disappears. Now, if the pupillary border were not in contact with the lens, a dark band, the shadow of the iris, would have intervened between the image and the border.

The structure of the iris cannot be clearly understood without reference to its development. This is treated elsewhere in this work, and it is only necessary to remark here that the pupil is the opening of the optic cup, which, it will be remembered, has, by the invagination of the optic vesicle, become two-layered, like the toy called the cup of Tantalus. (See Fig. 47.)

The two layers of the cup (*a*, *b*) are continued forward and unite at the pupillary border of the iris, constituting the black seam seen there.[1] The outer layer is pigmented throughout, the inner layer only where it forms the posterior surface of the iris. Together they constitute what is known as the *retinal portion* of the iris,[2] being not derived from the middle coat. That coat is, however, continued forward as an envelope of the optic cup, forming the anterior portion or stroma of the iris. This is, therefore, termed the *uveal portion*[3] of the iris. (Fig. 47, *c*.) The two portions retain certain characteristics of the coats from which they are derived, the retinal portion being essentially epithelial in character, the uveal portion composed of loose connective tissue, rich in blood-vessels, its anterior surface formed of flattened endothelium like its congener the posterior layer of the cornea, with which it is continuous at the angle of the anterior chamber.

At first the investment is continued from the iris about the lens, forming what is known as its vascular tunic,[4] evidently necessary for the nutrition of that organ while growing. The part of this tunic then seen in front appears as a continuation of the iris closing in the pupil, and is therefore called the pupillary membrane.[5] (Fig. 47, *d*; Fig. 48.) It usually disappears during the latter portion of intra-uterine life, but vestiges of it may remain even in adults as fine threads passing across the pupil. Stephenson[6] found vestiges of this structure sixty-eight times in three thousand four hundred and fourteen eyes examined, or nearly two per cent. It was more frequent in females. The vestiges did not interfere with sight or with the action of the pupil. They appear to occur more frequently in members of the same family. They do not arise from the margin of the

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[1] This arrangement of the doubling over of the layers of the iris appears to have been suspected before the microscope revealed it. Jacobus Sylvius speaks of it as reflected and doubled at the pupillary margin. "Choroides . . . ibi relicto foramine quam vocamus pupillam, reflexa, et quadamtenus duplata. . . ." In Hippocratis et Galeni physiologiæ partem anatomicam isagoge, Paris, 1555, l. i. cap. iv.

[2] Syn.: *pars retinalis iridis; pars iridica retinæ.*

[3] Syn.: *pars uvealis iridis; pars iridica uveæ.*

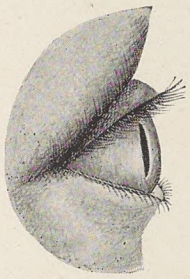
[4] Syn.: *tunica vasculosa lentis.*

[5] Syn.: *membrana pupillaris; m. capsulo-pupillaris;* capsulo-pupillary membrane; membrane of Wachendorf. Wachendorf first published a description of it in 1740. Albinus is said to have noticed it some years previously.

[6] Stephenson (Sydney). Concerning Persistent Pupillary Membrane and its Frequency. Trans. Ophth. Soc. United Kingdom, xiii., 1892–93, 139.

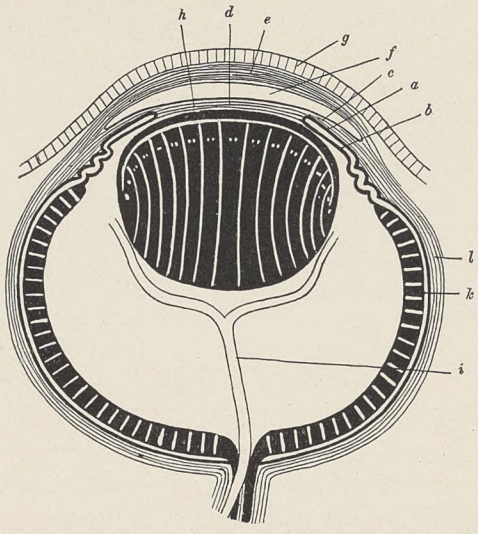
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FIG. 46.



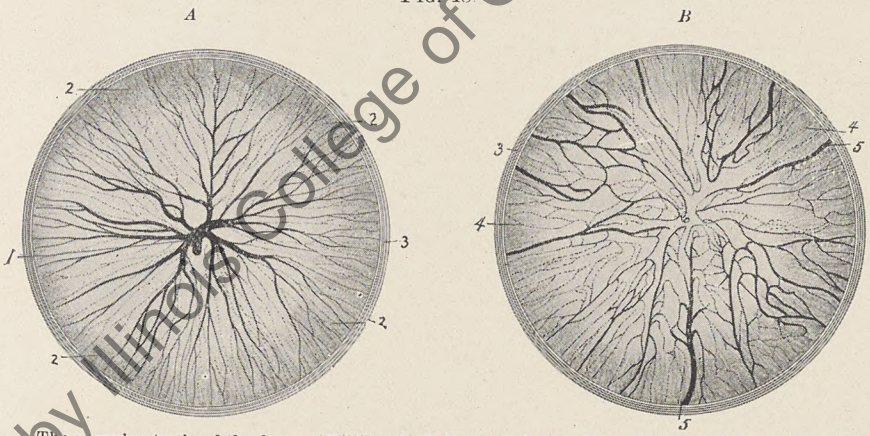
Iris and sclera viewed from the side. (Helmholtz.)

FIG. 47.



Development of the eye, shown diagrammatically.—*a*, *b*, outer and inner layers of the optic cup, forming the retinal portion of the iris; *c*, the uveal portion of the iris derived from the connective-tissue investment; *d*, a portion of that investment passing in front of the lens and forming the pupillary membrane; *e*, portion of the investment forming cornea; *f*, cleft in the investment forming anterior chamber; *g*, conjunctival epithelium; *h*, lens; *i*, hyaloid artery; *k*, retina; *l*, chorioid and sclera.

FIG. 48.



The vascular tunic of the lens. (Kölliker.)—*A*, its posterior surface; *B*, its anterior surface, forming the pupillary membrane. 1, hyaloid artery cut across; 2, 3, radiating vessels directed towards the equator of the lens; 4, the same vessels that have passed the equator and appear on the anterior surface; 5, venous trunks passing to the iris.

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pupil, but from the anterior surface of the iris, and can thus be distinguished from the inflammatory vegetations of iritis.

The following arrangement of the layers of the iris naturally follows from what has been said of its development:

A. *Iris Proper.*

1. Anterior endothelium.
2. Anterior boundary layer.
3. Stroma.
4. Basilar layer.

B. *Retinal Iris.*

5. Anterior layer of epithelium.
6. Posterior layer of epithelium.

Layers 2 and 4 are merely specially modified portions of the stroma.

The proper relations of these layers will become evident upon inspections of Figs. 49 and 50.

The *anterior surface* of the iris, being visible through the transparent cornea, imparts to eyes the characteristic color by which they are described. This color is due partly to the dark pigmented layer of the posterior surface showing through the thin stroma, partly to pigmented cells lying in the stroma itself. When these cells are absent or nearly so, and the iris is thin, the dark background shows through the semi-opaque stroma as blue, a phenomenon caused by interference, as is the color of the cloudless sky or the appearance of veins through a delicate skin. When the iris is thicker and the opacity greater this becomes modified to gray, and when pigment-cells are scattered in considerable numbers through the stroma the color assumes various shades of green, yellow, and brown, the deepest tints of brown being the so-called black eyes.

On close inspection it will be seen that the color is by no means uniformly distributed, but appears in irregular flecks or spots alternating with lighter tints. On this account Broca advises those who wish to note with accuracy the color of the eyes to observe them at the distance of one metre, so that the tints may blend. The color is also distributed in two zones concentric with the pupil,—an inner or pupillary [1] one, from one to two millimetres wide, darker in light eyes and lighter in dark eyes, and an outer or ciliary [2] one, from three to four millimetres wide, darker in dark eyes and lighter in light ones. The limit between the two is a zigzag or festooned series of ridges, the *lesser circle* [3] of the iris.

The distribution of the pigment varies greatly in different individuals, so much so that it has been proposed to make a systematic record of the pattern of the iris for the purpose of identifying criminals.[4] The varia-

[1] Syn.: *annulus iridis minor* or *internus* or *pupillaris;* sphincter zone; internal colored ring.

[2] Syn.: *annulus iridis major* or *externus* or *ciliaris;* external colored ring.

[3] Syn.: *circulus minor iridis.*

[4] See Bertillon (A.). La couleur de l'iris. Rev. scient., Paris, 1885, xxxvi. 65–73.

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tions are more numerous in the ciliary zone, which may be markedly striated with radiating lines or concentric zigzags. The pigment-cells may collect in spots, giving an appearance like a leopard's skin. Walker supposed these to be of a vascular character, resembling the congenital vascular tumors called nævi, and consequently named them *nævi iridis*. The human imagination has not neglected to exercise itself upon these flecks and markings, and we consequently find that strange characters are deciphered in the eye. Lavater mentions an iris on which an ace of spades could be seen; Borelli one in which the words *Loué soit Dieu* could be read; Tenon saw the letters T and V in different cases; in others the names of Charles XII., King of Sweden, and "Napoléon, empereur," or mystical Hebrew characters, have been found. More practical in their bearing are those cases sometimes reported in which the deposits of pigment simulate a second pupil, or a coloboma.

FIG. 51.

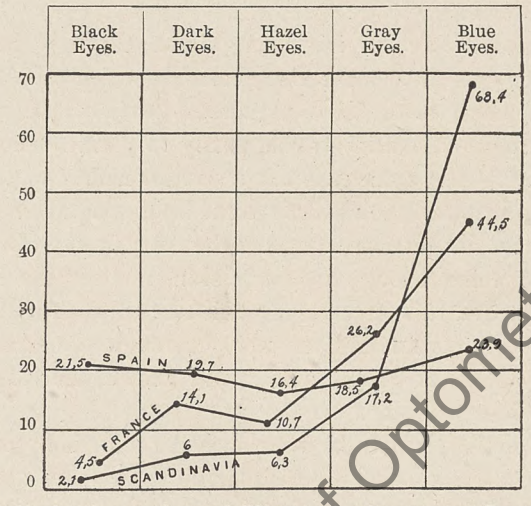


Diagram showing the prevalence of different-colored eyes among European peoples.

It was noticed by Aristotle that the eyes of new-born children are almost always blue. This is due to the fact that the pigment-cells of the stroma do not develop until some time after birth, the coloration not being complete until after the second year. In albinos not only is the stroma pigment wanting, but also that which lines the posterior surface. The iris consequently takes a pinkish color from the numerous blood-vessels it contains, and the eyes share with the rest of the face a deeper suffusion of color in blushing. This want of pigmentation is a serious disadvantage, as it causes great sensitiveness to a glare. Hence albinos shun bright light, and for this reason the Germans call them *Kakerlakken*, or cockroaches.

Considering the entire population of the world, we find that black eyes are by far the most numerous, these prevailing throughout the dark races, such as African, Indian, and Malay, and in a considerable proportion of the lighter ones, especially among peoples inhabiting tropical climates.

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FIG. 49.

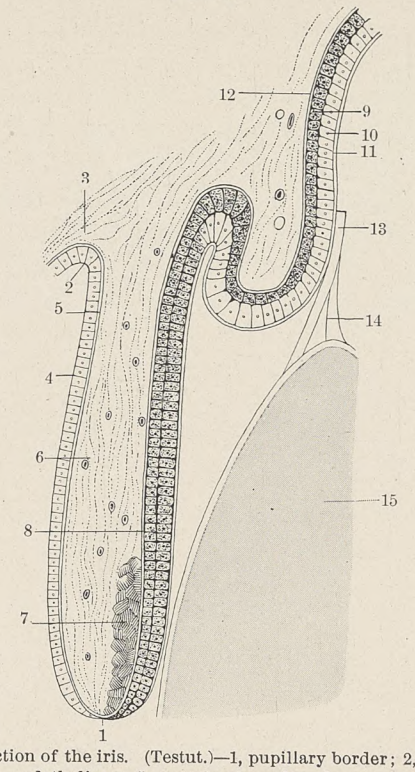
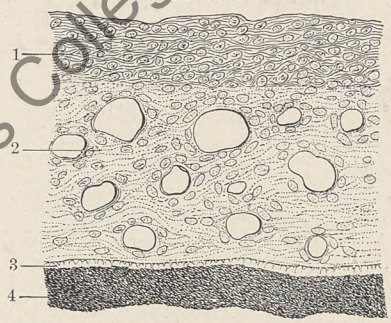


Diagram of a radial section of the iris. (Testut.)—1, pupillary border; 2, angle of the iris; 3, pectinate ligament; 4, anterior endothelium; 5, anterior boundary layer; 6, stroma; 7, fascicles of the sphincter pupillæ cut across; 8, basilar layer, in front of which lie the radiating fibres of the dilatator pupillæ, not here shown; 9, pigmented layer of the retina continued forward as the anterior layer of epithelium of the iris; 10, cubical epithelium of the ciliary portion of the retina continued forward as the posterior layer of epithelium of the iris; 11, internal limiting membrane continued forward upon the iris; 12, lamina basalis of the chorioid; 13, zonula; 14, zonular space or canal of Petit; 15, lens.

FIG. 50.



Horizontal section through the ciliary zone of the iris. (Gerlach.)—1, anterior endothelium; 2, stroma with vesseis cut across; 3, muscular layer containing the dilatator pupillæ; 4, pigmented layers.

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The color of the eyes usually corresponds with that of the hair and complexion, though not always, as it occasionally happens that blue eyes may accompany a bronzed skin, as in some Afghans (Fraser), and blue eyes and dark-brown hair are not a very unusual combination. It is considered by ethnologists that a close relation between eyes and complexion is more persistent in the lower races, and that want of agreement is an indication of mixed blood. In Europeans the iris may vary greatly in color, being generally blue in Scandinavians, Dutch, Belgians, North Germans, Irish, and Norman French; generally brown in the Mediterranean peoples. (See Fig. 51.)

FIG. 52.

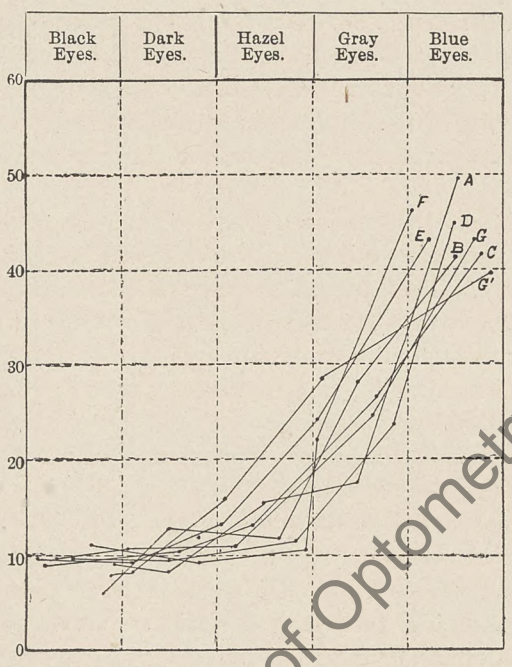


Diagram showing prevalence of different-colored eyes among soldiers native to the United States.—*A*, the six New England States; *B*, New York, New Jersey, and Pennsylvania; *C*, Ohio and Indiana; *D*, Michigan, Wisconsin, and Illinois; *E*, slave States, not including Florida and Georgia; *F*, Kentucky and Tennessee; *G'*, free States west of the Mississippi; *G*, slave States west of the Mississippi.

Beddoe[1] considers that the inhabitants of cities have generally darker eyes than those of the surrounding country. In a mixed population like that of the United States no great value can be attached to statistics of coloration. It may, however, be interesting to consider the proportion of light and dark eyes in different parts of the Northern States, as shown in 519,645 native enlisted men during the civil war.[2] This is shown in Fig. 52.

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[1] Beddoe (John). On the Testimony of Local Phenomena in the West of England to the Permanence of Anthropological Types. Mem. Anthro. Soc., Lond., 1865–66, ii. 37.

[2] Gould (B. A.) Investigations in the Military and Anthropological Statistics of the American Soldier. New York, 1869.

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Generally speaking, the two eyes of the same individual are the same in color, but it sometimes happens that one is blue or gray, while the other is dark (*yeux vairons* of the French). The color pales somewhat with advancing age, and many change during life as a result of pathological processes. In an inflamed eye the iris may change from blue to yellowish green, and if it becomes permanently thickened it may remain gray. Being very vascular, it is extremely prone to changes under inflammatory disturbances: hence a comparison of the two eyes often becomes of high importance as a diagnostic sign.

On viewing the anterior surface with a glass (see Fig. 53), its apparent uniformity disappears, and it is seen to be marked by striate elevations having a somewhat irregular character but a general radial direction. Those of the pupillary zone are fine and close, and are called by Zinn the *radii minores*. They are so arranged that contiguous ones unite at very acute angles, leaving between them deep spaces, at the bottom of which the fibres of the sphincter muscle, *s*, may be seen running concentrically about the pupil.

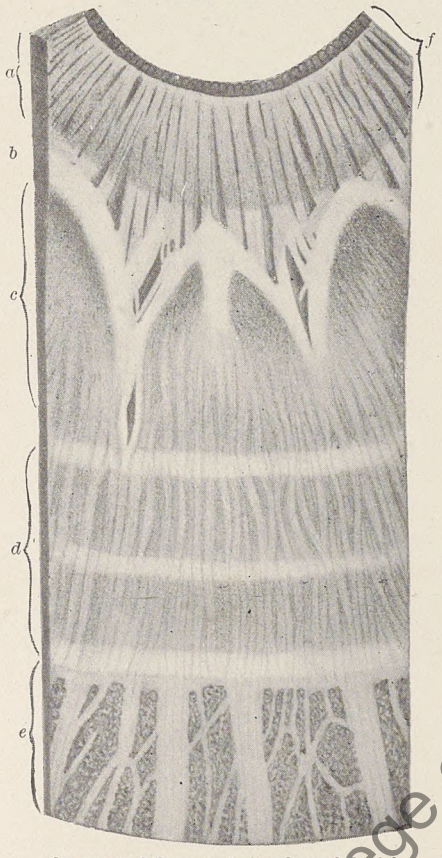
The lesser circle (*b*) is composed of plexiform elevations or trabeculæ that anastomose with each other in a wreath-like manner, forming a complete circumference. These are mainly the vestiges of the pupillary membrane, which in the fœtus was attached here. When this membrane became obliterated its vessels shrank away to cords of connective tissue. From this circle the fine radii of the pupillary zone pass towards the pupil and spurs extend outward into the ciliary zone. The prominence and shape of the trabeculæ vary with the degree of tension of the iris. (See Fig. 54.) Between them, but more frequent on the ciliary side, there are found oval or rhombic depressions called the crypts of the iris. These penetrate into the stroma, and are found to be the openings of lymph-spaces by which the aqueous humor can be removed from the anterior chamber. (Fuchs.) The trabeculæ may bridge them over or send out processes which pass into them and are lost on the floor.

The ciliary zone is divided by Fuchs into three concentric regions,—the first (*c*) smooth, not folded during dilatation of the pupil; the second (*d*) furrowed by arciform ridges that increase in depth during dilatation; the third (*e*) cribriform, showing depressions similar to the crypts. The first and second regions are about equal in width, and easily inspected in the living eye; the third is narrow and concealed in the living subject under the edge of the scleral bevel. The visible portion is marked by radial striæ corresponding to the vessels and nerves of the iris, the *radii majores* of Zinn. Between these appear dark spaces often filled with pigment. The furrows are one to seven in number, and are easily visible, describing incomplete arcs of circles concentric with the pupil.

The posterior surface of the iris is, except in albinos, deeply and uniformly colored, the pigmentary layer of the retina being not only continued upon it, but increased in thickness. As already stated, it rests by its lower

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FIG. 53.



Segment of the anterior surface of the iris ×20; pupil contracted. (Fuchs.)—*a*, pupillary zone; *b*, circulus minor; *c*, smooth, and *d*, folded part of the ciliary zone; *e*, marginal part of the same; *f*, sphincter muscle.

FIG. 54.



The same surface with pupil somewhat dilated. (Fuchs.)—Letters as in last figure.

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edge upon the surface of the lens, a contact which explains the importance of expanding the pupil in iritis, as otherwise inflammatory exudations are certain to glue the membrane to the lens, causing posterior adhesions or synechiæ. The extent of the contact was formerly a matter of dispute, some observers[1] holding that the entire posterior surface of the iris is applied to the lens and ciliary bodies, and that the posterior chamber exists only as a slit between two surfaces of contact; others, that there is always a cavity of some dimensions between the iris and the lens. The latter opinion is now universally accepted.

Heister[2] seems to have been the first to recognize the posterior chamber. The following evidence as to its existence seems conclusive. 1. In a fresh eye solidly frozen shortly after death, a thin ring of ice, the frozen aqueous humor, is found between the iris and the lens. This was carefully investigated by Petit in 1723.[3] Those who deny the existence of the chamber cite cases in which the ring was not found (possibly from evaporation of the aqueous humor or from want of care in the manipulation), and also hold that the chamber is formed post mortem as a result of the emptying of blood from the ciliary processes. 2. On suddenly jarring the head the upper part of the iris can be seen to tremble, which it would not do were it completely supported behind. 3. If a minute opening be made at the edge of the cornea and the aqueous humor partly evacuated, the iris will swell out towards the opening because of the pressure of the aqueous humor behind it. 4. A needle can be thrust with ease and certainty between the ciliary border of the iris and the lens. 5. Inflammatory adhesions occur almost invariably at the *pupillary* edge of the iris.

The modelling of the *posterior surface* differs somewhat from that of the anterior. (See Fig. 55.) A series of narrow radiating furrows separates flat ridges (the *structural folds* of Schwalbe) formerly thought to be continuous with the folds of the ciliary processes, but which are usually greater in number than those. These ridges are cut by a system of narrow concentric lines so that the entire surface is divided into small rectangular spaces, the arrangement resembling the serial succession of the kernels of an ear of corn as set upon the cob. (Fuchs.) Within the pupillary zone the number of radial furrows is increased (*contraction folds* of Schwalbe) and the concentric ones are nearly obliterated, so that the arrangement resembles a plaited ruffle. All furrows do not reach the pupillary margin, as several of the radial plaits may unite there, forming the bead-like heads already mentioned.

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[1] Among others the following may be cited:
Winslow (J. B.). Mém. de l'acad. royale des sciences, 1721.
Stellwag von Carion. Zeitsch. d. Gesell. d. Aerzte z. Wien, 1850, vi. 133.
Cramer. Het Accommodatievermogen der Oogen. Haarlem, 1853, p. 67.
Helmholtz (H.). Physiologische Optik. Leipzig, 1867, p. 19.
Sappey (P. C.). Anatomie descriptive. Paris, 1877, iii. 820.

[2] Heister (L.). Compendium anatomicum, 1819.

[3] Mém. de l'acad. royale des sciences, 1723.

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The *pupil*,[1] which Berger[2] picturesquely calls *janitrix oculi*, is normally round[3] in man, whatever may be its state of contraction or dilatation. This is, however, by no means the case with all animals. In many reptiles, fishes, and amphibians, and in some birds, it contracts to a vertical slit. In mammals it is not invariably round, being in ungulates (horse, ox) transversely oval contracting to a horizontal slit; in many of the felidæ, or cat tribe, contracting to a vertical slit and showing during expansion various elliptic or lozenge-shaped forms.

As excess of light injures the retina, and too divergent rays impair the definition of images thereon projected, the pupil contracts and expands during life according to the necessities of vision.[4] This is a reflex phenomenon dependent on the action of light upon the retina, and not caused, as was formerly thought, by rays falling upon the iris.[5] If a bright light passing through an aperture smaller than the pupil reaches the otherwise shaded eye, no effect is produced unless it penetrates to the retina, and when that occurs the pupil at once contracts. In man, stimulation of a single eye affects both pupils simultaneously, and any difference in their size may at once be considered as of pathological origin.

Long before Marshall Hall established our knowledge of reflex movements, similar theories were applied to these phenomena. Thus Morgagni[6] supposed that the retina, excited by light, conveyed its vibrations to the

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[1] From L. *pupilla*, a little girl or doll, probably because of the diminutive image of the observer that is reflected from the cornea on looking at the black background of the pupil. *Kindlein* for pupil is found in old German works, and the Greek κόρη is used for both girl and pupil. Isidorus (A.D. 636) says, "Vocatur autem pupilla quod sit pura atque impolluta ut sint puellæ."

Syn.: from its appearance, *nigrum oculi;* the apple of the eye (used as a comparison for something to be carefully kept from injury, Deut. xxxii. 10, Ps. xvii. 8, Prov. vii. 2, Zech. ii. 8). From its necessity for vision, the sight of the eye; ἡ ὄψις (Rufus Ephesius); *visio*, *fenestra*, or *lumen oculi; Sehe* or *Seheloch*, G.

[2] Bergerus (J. G.). Physiologica medica. Vitembergæ, 1701.

[3] Oval pupils are occasionally seen in man. Cases are cited as follows:

Plempius (V. P.). Ophthalmographia, l. iii. cap. viii.

Tode (J. C.). Soc. med. Havn. Collect., 1775, ii. 145.

Hagström. Abh. d. schw. Acad., xxxvi.

Ephem. nat. cur., viii. 34.

Archiv f. die Physiologie. Halle, v. 63.

Richter's Chir. Bibl., ii. 58; iv. 230; vii. 104.

Foucher (Rev. méd.-chir. de Paris, 1852, xii. 207) found thirty-four cases out of one hundred and fifty-four in which the pupil was more or less elliptical.

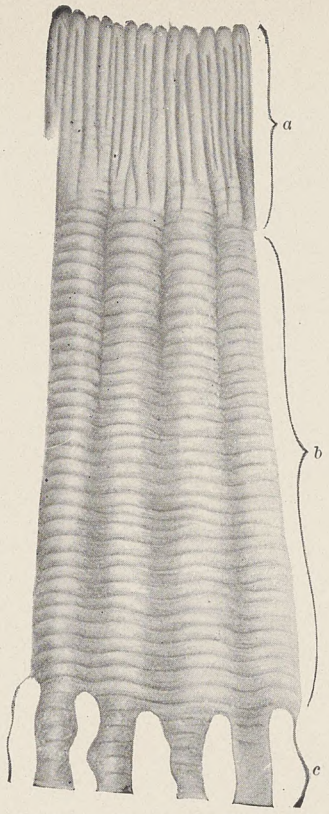
[4] This movement was apparently known to Galen. (De usu partium, lib. x. cap. v.) The Arabian physician Rhazes (A.D. 852–932) was first to note its connection with the intensity of light. He says, "In [uveæ] medio in loco scilicet ubi grandineo [*i.e.*, crystallino] opponitur humori, est foramen quod quandoque dilatur, quandoque constringitur prout grandineo humori causa luminis necessarium fuit. . . . Hoc foramen est pupilla." Ad Almansor, lib. i. cap. viii.

[5] See, for experimental proof of this, Zinn (J. G.), De motu uveæ, 1757; Müller (J. R.), De irritabilitate iris hincque pendente motu pupillæ, Basil., 1760, p. 9 *et seq.;* Fontana (Felice), Dei moti dell' iride, 1765.

[6] Epistola anatomica, xvii. 48.

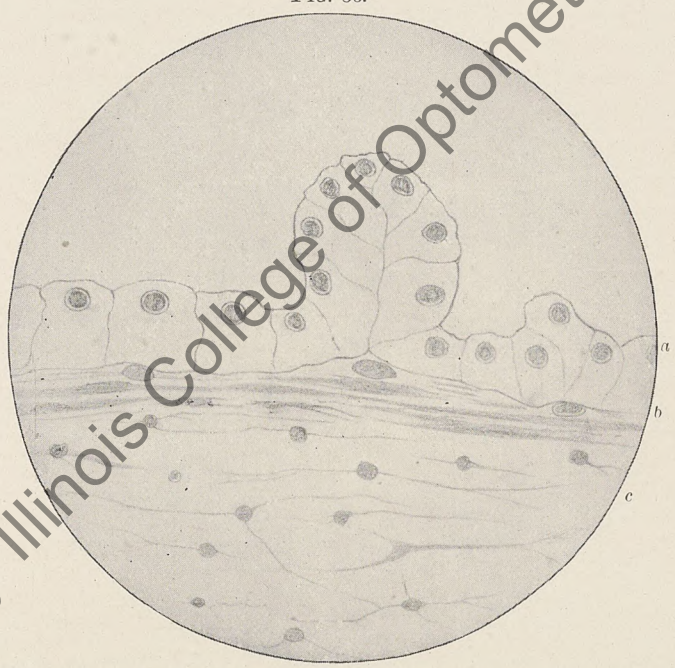
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FIG. 55.



Segment of the posterior surface of the iris × 25; medium dilation of the pupil. (Fuchs.)—*a*, pupillary zone; *b*, ciliary zone; *c*, ciliary processes.

FIG. 56.



Reproduction of photomicrograph showing a portion of a radial section of the iris after bleaching with euchlorine. (Juler.)—*a*, posterior epithelium; *b*, layer of muscle-fibres constituting the dilatator pupillæ; *c*, stroma. The oval cells with normal nuclei between *a* and *b* probably represent the *anterior* epithelial layer.

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iris, and Blumenbach [1] actually anticipated the modern theory of nervous action by supposing the vibrations of light to be conveyed to a *sensorium commune*, which in turn affected the iris.

From an early period anatomists have attempted to determine the essential structures upon which these movements depend. The investigation is one of unusual difficulty, owing to the fact that they are covered over and greatly obscured by the pigmented cells of the iris, which cannot be removed without damaging to some extent the subjacent tissues. It is not surprising, therefore, that a number of conflicting views should have been held regarding these structures, and that a long and sometimes acrimonious controversy concerning them should have lasted up to the present time.

The earliest view was that the iris enlarged and contracted by the filling of its fibres (vessels, nerves, etc.) with some fluid, either the *pneuma* [2]—animal or vital spirits—of the old physiologists, or blood. Fabricius ab Aquapendente considered its properties those of erectile tissue.[3] Méry [4] had a similar view, holding that the active state was during contraction of the pupil, dilatation being caused by the elasticity of the posterior membrane, thus explaining the dilatation after death. Vieussens [5] described a "vasculo-lymphatic-nervous sphincter" at the pupillary margin, and Ferrein,[6] Haller,[7] Zinn [8] in part, Fontana,[9] and Sömmering,[10] also maintained the erection theory. Even during the present century many [11] have ascribed the movements either wholly or in part to an influx and efflux of blood. The question appears to have been finally settled by the experiments of Brown-Séquard,[12] who showed that the pupillary orifice is but slightly narrowed by injecting the blood-vessels of the iris.

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[1] De oculis leucæthiopium et iridis motu. Gottingæ, 1786.

[2] Galen, loc. cit.

[3] Tract. anat. de oculo, aure et larynge, 1613, p. 58. After comparing the iris to the muscle of the heart, which he considers has a special faculty of its own, he continues, "Melius autem forte fuerit virilis pudendi motui uveæ foraminis motum assimilare; ita ut sicuti penis per insitam quandam facultatem erigitur."

[4] Mém. de l'acad. royale des sciences. Amsterdam, 1704, p. 353.

[5] Traité nouveau des liqueurs du corps humain. Toulouse, 1715, p. 211.

[6] Mém. de l'acad. royale des sciences, 1741, p. 495.

[7] Primæ lineæ physiologiæ. Gottingæ, 1751. Elementa physiologiæ, 1763, xvi., ii. p. 371.

[8] Descriptio anatomica oculi humani. Gottingæ, 1755.

[9] Dei moti dell'iride. Lucca, 1765.

[10] In his commentary on Haller's Primæ lineæ, Berlin, 1788, p. 391.

[11] Portal (A.). Cours d'anatomie médicale. Paris, 1804.

Gaddi (P.). Argomenti dimostrativi della fondamentale struttura vascolare dell' iride. Raccoglitore, Fano, 1845, xvi. 258–266.

Guarini (L.). L'iride se muove per simplice erettismo vascolare, oppure per opera de fibre muscolari? Ann. univ. de med., Milano, 1844, cxii. 21–48.

Letheby. On the Structure and Movements of the Iris. Royal London Ophth. Hosp. Rep., London, 1859, ii. 18–20.

[12] Compt.-rend. Soc. de biol., 1849. Paris, 1850, i. 116–118.

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Other and more chimerical views with regard to the cause of the movements have been occasionally advanced. Weitbrecht[1] believed them to be due to the expansion and contraction of the vitreous body. Della Torre[2] ascribed them to the contractile power of the very numerous nerves with which the iris is supplied.

Blumenbach[3] held that there was some special vital property in the tissue of the iris that endowed it with contractility, but that it was not muscular. Essentially similar views were maintained by other anatomists.[4]

Since, however, the movements of the iris are like those produced by muscle-fibres, it was early thought by some to be a muscular organ. Thus we find that Avicenna,[5] the chief of the Arabian school (A.D. 980–1036), calls it "*lacertus motus pupillæ*," and Descartes[6] held a similar view. This was based, however, on theoretical grounds, as no means then existed for demonstrating muscular fibres.

The arrangement and direction of the fibres were naturally matters of discussion. The radial folds formed by the vessels resembled to the naked eye muscle-bundles, and we accordingly find that almost without exception those who upheld the muscular nature of the organ believed it to be arranged radially. Vesling[7] held that fibres were prolonged into the iris from the ciliary processes. Riolan[8] and Drélincourt[9] seem to have had a clear idea of such radial fibres without suspecting any orbicular ones, and Valsalva,[10] O'Halloran,[11] and Zinn[12] all expressly deny orbicular fibres, while admitting radial ones.

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[1] Comm. Petrop., xiii. 349.

[2] Nuove osservat. microscopiche, p. 68.

[3] Op. cit.

[4] Dömling. Arch. f. d. Physiol. Halle, 1802, v. 335.

Bichat (M. F. X.). Anatomie descriptive. Paris, 1801–03, ii. 444.

Grapengieser. Asklepeion, 1811, p. 1314.

Weber (E. H.). De motu iridis. Lipsiæ, 1821.

Rudolphi (K. A.). Physiologie. Berlin, 1821–28, ii. 218.

Arnold (Fr.). Anatomische und physiologische Untersuchungen über das Auge des Menschen. Heidelberg and Leipzig, 1832, p. 74.

[5] Canon. Tr. 3, Fen. 1, c. i.

[6] "Ce trou [la prunelle] n'est pas toujours de mesme grandeur, car la partie de la peau dans laquelle il est, nageant librement dans l'humeur, qui est fort liquide, semble estre comme un petit muscle, qui s'élargit ou s'étrécit par la direction du cerveau, selon que l'usage le requiert." L'Homme, Paris, 1664, p. 39.

[7] Syntagma anatomica. Patavii [Padua], 1659, p. 202.

[8] Anthropographia et osteologia. Parisii, 1626, pp. 416–429.

[9] Opera varia, 1693.

[10] Opera. Venetiis, 1741.

[11] A New Treatise on the Glaucoma, or Cataract. Dublin, 1750, p. 74.

[12] Descriptio anatomica oculi humani, 1755, p. 89. He also states that he bases his conclusions rather on the known properties of vascular tissue than on actual demonstrations. "Dum autem phænomena, vascula, molem nervorum iridem adeuntium, ejusque analogiam cum aliis partibus corporis humani musculosis attentius considero, parum abest, quin ad credendum adducar, fibras musculosas reliquis vasculis et nervulis in anteriore facie iridis intermistas esse."

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Berger[1] appears to have been the first to recognize clearly the existence of fibres encircling the pupil. Ruysch[2] mentioned and figured them shortly after, with some doubt, and they were soon recognized by a large number of anatomists,[3] most of whom seem to have been led rather by the known functions of the organ than by any special anatomical appearances noted. All these authors admitted the existence of the radial or dilatator fibres without question. Demours,[4] however, declared that the radial fibres were not muscular.

The first careful microscopical demonstration of the sphincter was made by Maunoir[5] in birds. Treviranus[6] afterwards showed its fibres to be striated in those animals. Valentin[7] found them smooth in mammals, and Krohn,[8] Lauth,[9] and Schwann[10] confirmed this for man. Since these inves-

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[1] "Duplex quoque idem est circulus major, alter, qui desinit, ubi fibræ processus ciliaris terminantur, et reflectuntur arteriolæ, alter multo minor, qui ad pupillam desinit, et ex fibrillis circularibus, in orbemque scite flexis, et annuli in modo circumductis, constructus videtur." Physiologia medica. Vitembergæ, 1701, p. 405, Amstelodami, 1702.

[2] Thesaurus anatomicus, ii. Amstelodami, 1702, pl. i. fol. 5.

[3] See, among others:

Maitrejan (Antoine). Traité des maladies de l'œil, 1707.

Morgagni (J. P.). Adversaria anatomica omnia, 1719, i. 337, vi. 88.

The same. Epistola xvi., No. 9.

Heister (Laurenz). Compendium anatomicum, 1727, p. 215. He describes these fibres as the *sphincter pupillæ*.

Palfyn (J.). Anatomie chirurgicale. Paris, 1734.

Lobé (J. P.). De oculo humano. Lugd. Bat., 1742, p. 22.

Boerhaave (H.). Prælectiones academicæ, 1742–45.

Petsche (J. Z.). In Haller's Disputationes anatomicæ. Gottingæ, 1751, vi. 768.

Mauchart (B. D.). De mydriasis. In Haller's Disputationes chirurgicales, 1755, i. p. 558. Has an excellent description of the preparation of the iris by brushing off the posterior pigmented layer, and compares the muscle-fibres to those of blood-vessels.

Winslow (J. B.). Exposition anatomique de la structure du corps humain, 1757.

Porterfield (William). A Treatise on the Eye. Edinburgh, 1759, i. 153.

Gataker (Thomas). An Account of the Structure of the Eye. London, 1761, p. 52.

Deverney (J. G.). Œuvres anatomiques. Paris, 1761, i. 146.

Whytt (Robert). Essay on the Vital and other Involuntary Muscles of Animals. Edinburgh, 1763. He appears to have been the first to name the radial fibres the *laxator* or *dilatator pupillæ*.

De St. Yves (Charles). Nouveau traité des maladies des yeux, 1767, p. 12.

Janin de Combe Blanche (Jean). Mémoires et observations anatomiques, physiologiques et physiques sur l'œil. Lyon, 1772, p. 8.

Cheselden (William). Anatomy, 1792.

Monro (Alexander). On the Brain, Eye, and Ear, 1797, p. 112.

[4] Dissertation sur le mécanisme des mouvements de la prunelle où l'on examine quelle est la structure et la manière d'agir des fibres droites de l'uvée. Recueil des pièces par des savants étrangers, publié par l'Académie des Sciences.

[5] Mémoire sur l'organisation de l'iris. Paris, 1812.

[6] Vermischte Schriften, 1820, iii. 167.

[7] Repertorium f. Anat. u. Physiol., 1837, p. 248.

[8] Ueber die Structur der Iris der Vogel und ihren Bewegungsmechanismus. Arch. f. Anat., Physiol. u. wissensch. Med., Berlin, 1837, p. 379.

[9] Institut., Nos. 57, 70, 73.

[10] In Joh. Müller's Handb. d. Physiologie, 1840, ii. 36.

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tigations the existence of the *sphincter pupillæ*[1] has never been seriously questioned. It consists of a well-marked, flat ring of plain, muscular fibres about one millimetre in width,[2] lying next the pupillary margin. It is from 0.07 to 0.1 millimetre thick, and lies behind the vessels against the basilar layer. At its outer edge it is looser in texture, certain fibres arching away from the ring and assuming a radial direction.

With regard to the existence of true, radiating muscle-fibres constituting a veritable *dilatator pupillæ*[3] much controversy has arisen. The early observers seem to have based their conclusions upon theoretical grounds rather than upon actual observation of the structure in man. After its description by Brücke,[4] Kölliker,[5] and Budge,[6] its presence was generally conceded, although these authors did not fully agree as to the details of its situation, origin, and insertion. In 1864, however, its existence was again denied by Grünhagen, who has up to the present time so persistently opposed it that his views have been widely accepted.[7] On the one side are found Henle,[8] Kölliker,[9] Luschka,[10] Merkel,[11] Iwanoff,[12] Faber,[13] Sappey,[14] Dogiel,[15] Gerlach,[16] Retzius,[17] Schäfer,[18] Böhm, and v. Davidoff,[19] all of

[1] Syn.: *contractor pupillæ; sphincter iridis; musculus circularis iridis.*

[2] This is the dimension given by Brücke, Budge, Henle, Luschka, Stöhr, and others. Kölliker gives it as 0.56 millimetre; Faber as 0.8 millimetre; Merkel as from 0.8 to 1 millimetre.

[3] Syn.: *laxator pupillæ; dilatator iridis; musculus radialis iridis.*

[4] Anatomische Beschreibung des menschlichen Augapfels. Berlin, 1847, p. 18.

[5] Mikroskopische Anatomie. Leipzig, 1854, ii.

[6] Ueber die Bewegung der Iris. Braunschweig, 1855.

[7] Ueber Irisbewegung. Arch. f. path. Anat., etc., Berlin, 1864, xxx. 481–524.

Ueber das Vorkommen eines Dilatator pupillæ in der Iris des Menschen und der Säugethiere. Zeitschr. f. rat. Med., Leipzig u. Heidelb., 1866, 3 R. xxviii. 176–189.

Zur Iris-Bewegung. Arch. f. d. ges. Physiol., Bonn, 1870, iii. 440–448.

Zur Frage über die Iris-Musculatur. Arch. f. mikr. Anat., Bonn, 1873, ix. 286–292.

Ueber die hintere Begrenzungschichte der menschlichen Iris. Ibid., 726–729.

Ueber die Muskulatur und Bruchsche Membran der Iris. Anatomischer Anzeiger, 1888, iii. 27.

[8] Handbuch der systematischen Anatomie des Menschen. Braunschweig, 1873, ii. 654.

[9] Handbuch der Gewebelehre des Menschen, 5te Aufl., 1867, p. 667.

[10] Anatomie des Menschen. Tübingen, 1867, iii., Abth. 2, p. 416.

[11] Die Muskulatur der menschlichen Iris.

[12] Gräfe u. Sämisch's Handbuch. Leipzig, 1874, i. 283–287.

[13] Der Bau der Iris des Menschen und der Wirbelthiere. Leipzig, 1876.

[14] Anatomie descriptive. Paris, 1877, iii. 785.

[15] Ueber den Musculus dilatator pupillæ bei Säugethieren und Vögeln. Centralb. f. d. med. Wissensch., Berlin, 1869, vii. 337–340.

Ueber den Musculus dilatator pupillæ bei Säugethieren, Menschen und Vögeln. Arch. f. mikr. Anat., Bonn, 1870, vi. 89–99.

Neue Untersuchungen über den pupillerweiternden Muskel der Säugethiere und Vögel. Arch. f. mikr. Anat., Bonn, 1886, xxvii. 403.

[16] Handbuch der speciellen Anatomie des Menschen. München und Leipzig, 1891, p. 199.

[17] Zur Kenntniss vom Bau der Iris. Biologische Untersuchungen, N. F., 1893, vii.

[18] Quain's Elements of Anatomy. London, 1894, vol. iii., part iii., pp. 32, 33.

[19] Histologie des Menschen. Wiesbaden, 1895, p. 336.

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whom, after careful examination, affirm the existence of the dilatator; on the other, Grünhagen, Fuchs,[1] Boe,[2] Koganei,[3] Retterer,[4] Schwalbe,[5] Debierre,[6] and Testut,[7] who deny it.

The matter under contention is the interpretation of the appearances in the posterior portion of the stroma of the iris. Here are seen a large number of nuclei resembling those of unstriped muscular fibre lying in a tissue that appears to be radially striated. Those who deny the existence of the dilatator hold that these nuclei belong to the epithelial layer, and that no proper muscular fibre exists; while, on the other hand, many observers hold that fibres are demonstrable, and even that they can be isolated.

One of the most recent and apparently conclusive proofs of the existence of the muscle was made by Juler at the Ophthalmological Congress at Edinburgh in 1894.[8] He exhibited specimens of the iris in which the pigmented epithelium of the posterior surface had been bleached by euchlorine, so that the subjacent structures were plainly visible. In front of the epithelial layer was seen a continuous layer of muscular fibres two or three deep. The fibres were fusiform, with rod-shaped nuclei, that showed no local bulging such as is often seen in connective-tissue fibres. (See Fig. 56.)

Juler considers them absolutely identical with unstriped muscular fibres found elsewhere. They appear to run from the pectinate ligament to the sphincter, with which they blend.

Besides the anatomical proofs of the existence of two orders of muscular fibres in the iris, there are others, seemingly conclusive, that depend upon physiological experimentation. There is apparently an antagonism existing between the nerve-supply of the sphincter and that which presides over the dilatation of the pupil. Herbert Mayo[9] showed that the sphincter is supplied by the oculo-motor nerve. Section of the nerve paralyzes the muscle and increases the size of the pupil, while stimulation of it causes contraction of the pupil. On the other hand, Petit[10] discovered that section of the sympathetic in the neck apparently paralyzes the apparatus for dilatation, as it somewhat diminishes the size of the pupil, and Biffi[11] showed that stimula-

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[1] Beiträge zur normalen Anatomie der menschlichen Iris. Arch. f. Ophthalmologie, Berlin, 1885, xxxi., Abth. iii. pp. 39–86.

[2] Quelques recherches sur la couche pigmentaire de l'iris et sur le soi-disant muscle dilatateur de la pupille. Arch. d'ophtalmologie, Paris, 1885, v. 311.

[3] Arch. f. mikr. Anat., Bonn, 1885.

[4] Bull. Soc. de Biologie, 1885.

[5] Anatomie der Sinnesorgane. Erlangen, 1887, 205–209.

[6] Sur le muscle de l'iris de l'homme. Comptes-rendus de la Soc. de Biologie, Paris, 1888, 8 sér., v. 361.

[7] Anatomie humaine. Paris, 1894, iii. 149, 150.

[8] A Contribution to the Anatomy and Physiology of the Iris. Trans. Eighth Internat. Ophthalm. Congress, Edinburgh, 1894, p. 67.

[9] Jour. de physiol. expér., Paris, 1823, iii. 349.

[10] Mém. de l'acad. royale des sciences, 1727, p. 1.

[11] Biffi (Serafino). Intorno all' influenza che hanno sull' occhio i due nervi grande simpatico e vago. Dissert. inaug., Par., 1846.

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tion of the same nerve dilates the pupil. It is, therefore, natural to suppose that this nerve supplies fibres having a dilating function.

In 1852, Claude Bernard[1] discovered that the cervical sympathetic contained vaso-constrictor fibres, and the opponents of the dilatator then held that it was the action of these fibres upon the vessels of the iris, causing either a decrease of turgescence or a contraction of radial arteries, that effected the dilatation of the pupil. To this it may be replied that dilatation of the pupil may be caused by excitation of the cervical sympathetic after an animal has bled to death, that contraction of the blood-vessels in other parts of the head is not synchronous with the dilatation of the pupil, and that atropine has been seen to dilate the pupil in white rats without causing any change in the blood-vessels.[2] Further, a direct examination of the iris during the stimulation of the sympathetic in the neck shows that contraction of the vessels does not occur until after the pupil dilates. (Langley and Anderson).[3]

Grünhagen and others[4] have also maintained that the dilatation occurring after excitation of the cervical sympathetic may be due to inhibition of the sphincter, the basilar layer of the iris proper (the posterior portion of the stroma already alluded to) being a highly elastic tissue that at once dilates the pupil as soon as the tension of the sphincter is abolished.

Langley and Anderson found no evidence of inhibition of the sphincter, as excitation of the sympathetic caused contraction of sectors of the iris severed from the remainder by radial incisions, and this without the least relaxation in the tone of the pupillary border. When such a sector is kept in an extended state for a short time it does not retract on being released, as it would did it contain sufficient elastic tissue to act as an efficient dilatator. Neither does it retract after complete death of the iris muscles when the sphincter portion is removed. Besides, a local stimulation upon the sclera or by means of the sympathetic (all the ciliary nerves but one being cut) causes a local dilatation with contraction of the sphincter, and also drags over to the stimulated side that part of the iris opposite the stimulus. (See Fig. 57.) This cannot be explained by Grünhagen's hypothesis.

The combined anatomical and physiological evidence of the existence of a radially arranged, dilatator muscle now appears conclusive.

The causes of the movements of the iris may be briefly summarized as follows: contraction of the pupil may occur not only from the stimulation of the retina by light, as in excess of illumination, but also from the gen-

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[1] Comptes-rendus de la Soc. de Biol., 1852, Paris, 1853, iv. 155.

[2] Zeglinski (N.). Experimentelle Untersuchungen über die Irisbewegung. Arch. f. Anat. u. Physiol., Abth. i., 1855, p. 1.

[3] Langley and Anderson. On the Mechanism of the Movements of the Iris. Jour. of Physiol., Cambridge, 1892, xiii. 544–597.

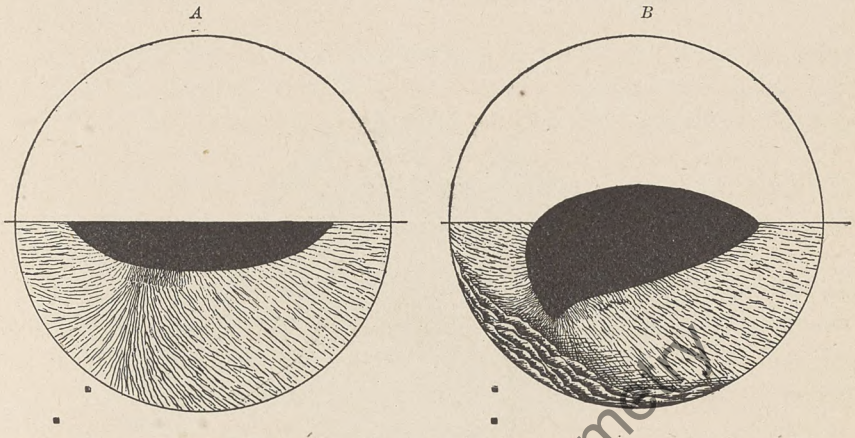
[4] Grünhagen and Samkowy. Arch. f. d. ges. Physiol., 1875, x. 165.
François-Franck. Travaux de la laboratoire de M. Marey, 1880, iv. 55.
Gaskell. Jour. of Physiol., Cambridge, 1886, vii. 38.

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eral stimulation of electricity or strychnine; from the deadening of the reflexes, as in sleep, coma, narcosis, and the first stages of chloroform- or alcohol-poisoning; from the topical application of myotics, such as eserine (physostigmine) and pilocarpine; from central disorders, such as encephalitis and meningitis; from local disorders, such as iritis and many affections of the globe; from increase of blood-pressure, as in forced expiration, deficiency of the aqueous humor, or anything else causing congestion. Contraction also appears to be associated with certain movements of the eye. Thus it occurs in accommodating for near objects[1] and in turning the eye inward.

Dilatation occurs from an opposite set of causes, such as deficiency of

FIG. 57.



Effect of local stimulation of the sclera in the cat. (Langley and Anderson.)—*A*, first stage, contraction of the sphincter; *B*, second stage, radial contraction synchronous with contraction of the sphincter. The two dots indicate the position of the stimulating electrodes.

light; anything tending to make the retina insensitive, such as amblyopia or amaurosis; the application of mydriatics, such as atropine, daturine, or hyoscyamine; depression of the nervous system, as in fright, shock, fatigue, the latter stages of chloroform- or alcohol-poisoning; lowering of the blood-pressure, as in the application of cocaine; in dyspnœa; in strong muscular exertion; in excessive distention of the anterior chamber. Accommodation for distant objects also dilates the pupil.

When fully contracted the pupil is so small that it is easy for it to be totally occluded by inflammatory exudations; hence the importance of dilating it during iritis. Its diameter varies somewhat with age. Closely contracted in the newly born, it is rather large in children whose reflexes are active, somewhat smaller in adult life, and still more reduced in old

[1] Hence Haller (Elementa physiologiæ, 1743, v. 516), Morton (Am. Jour. Med. Sci., November, 1831), and others held that accommodation is produced by adjustment of the pupil. This is incorrect, for accommodation is not affected by viewing objects through a hole smaller than the pupil.

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age. In the aged the iris is somewhat stiffened by the increase of connective tissue, and it therefore reacts less readily.

The *nerves* of the iris are derived from the ciliary plexus, which has already been described in connection with the ciliary muscle. They are at first medullated, and quickly reunite within the ciliary zone to form another or iridian plexus, which is denser as it approaches the sphincter. Three orders of fibres are derived from this plexus,—first, pale, non-medullated fibres, apparently belonging to the sympathetic, that pass backward towards the dilatator and are believed to supply it; second, medullated fibres, apparently sensitive, that pass to the anterior surface; third, medullated fibres that pass to the sphincter and probably give it its motor influence. Certain vaso-motor fibres supply the coats of the vessels. There are no ganglion-cells in the iris, as was formerly supposed.

FIG. 58.



Arteries of the iris. (Sappey.)—1, 1, long posterior ciliary arteries; 2, 3, their branches of bifurcation; 4, recurrent arteries destined for the chorioid; 5, 5, 6, 6, anterior ciliary arteries anastomosing with the long ciliary to form the greater arterial circle of the iris; 7, the lesser arterial circle of the iris.

The tactile sensibility of the iris is not great. Operations upon the membrane are not very painful if traction is avoided.

The *arteries* of the iris are derived from the long posterior ciliary and the anterior ciliary arteries. The long posterior ciliary, two in number, arise from the ophthalmic artery where it lies below the optic nerve, and penetrate the sclera near its junction with that nerve. Their course within the chorioid has already been described. (See Fig. 35; Fig. 36, *b;* Fig. 58, 1, 1.) Just before reaching the posterior border of the ciliary muscle, at four to seven millimetres behind the cornea, each bifurcates into an ascending and a descending branch; these soon assume a direction parallel to the equator, the arteries of opposite sides finally anastomosing with each other and with the anterior ciliary arteries. The latter vessels (see Fig. 35; Fig. 36, *c;* Fig. 58, 5, 5, 6, 6), six to eight in number, are derived

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from the muscular or lacrymal branches of the ophthalmic artery, and pierce the sclera at or near the annular ligament. Uniting with the branches of the long posterior ciliary, they form a vascular anastomosis about the ciliary border of the iris between the two portions of the ciliary muscle. This is known as the greater arterial circle of the iris.[1] (See Figs. 35, 36, and 58.)

From the concavity of this arcade arterioles pass radially towards the pupil, lying in the stroma and dividing dichotomously with frequent cross-unions in a way which has been compared to the behavior of the vasa intestini tenues of the mesentery. (Morgagni, Zinn.)

At the periphery of the sphincter the branches form a fine circular mesh-work, the lesser arterial circle of the iris.[2] (Fig. 58, 7.) It is from this that branches are given off during fœtal life to supply the pupillary membrane.

The *veins* of the iris arise from the capillary net-work of the sphincter and from the delicate branchlets of the anterior surface, and gather into trunks that run meridionally backward through the orbiculus ciliaris, to empty into the vorticose veins.

The vessels of the iris are deficient in muscular fibres, but have unusually thick coats of circular connective-tissue fibres. (Böhm and von Davidoff.)

There are no proper *lymphatics* in the iris, but very numerous lacunar spaces, by which the lymphatic circulation is kept up, occur in the stroma. In the crypts of the anterior surface these present open mouths, and the aqueous humor doubtless passes freely by means of these spaces into the general circulation.

THE INNER OR NERVOUS COAT.[3]

Formed by an outgrowth from the brain,—that is to say, by the primitive optic vesicle or ophthalmencephalon,—the inner coat is in many respects analogous to the cerebral cortex.[4] It contains the essential portion of the

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[1] Syn.: *circulus arteriosus iridis major.*

[2] Syn.: *circulus arteriosus iridis minor.*

[3] Syn.: *tunica interna; t. nervosa;* retina; *Netzhaut*, G.; *rétine*, F. The term retina is derived from L. *rete*, a net.

Hyrtl (Onomatologia anatomica, p. 452) comments on the absurdity of this name, as the retina is not a net. The name first appears in a translation of the Canon of Averroes made by Gerardus Cremonensis. The passage is as follows: "Extremitas nervi concavi [the optic nerve, so called because he considered it hollow] comprehendit vitreum [the vitreous body], sicut rete comprehendit venationem [the catch], quapropter nominatur retina." (Lib. iii., fen. 3, tract. i., cap. i.)

Galen used the term *ἀμφιβληστροειδής* (*χιτών*), which indicates primarily an investment (from *ἀμφιβάλλω*, to throw around), secondarily a net which invests the captured fish. His Arabic translators took it in the latter sense only, and called it *rescheth*, meaning *retiformis*. To express this Gerardus invented the well-sounding but barbaric term *retina*.

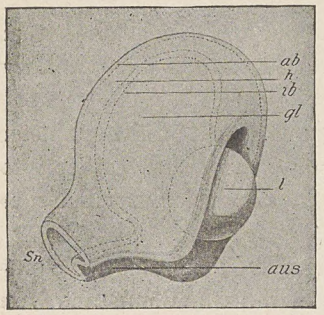
[4] Casserius says, "Retina convoluta cerebri substantiæ similis." Pentæsthesion, l. 5, tab. v., Fig. 9.

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organs of vision,[1] the other coats being subsidiary to it and serving for its protection and nourishment. Originally vesicular in form, with the optic nerve for a pedicle, the development of the lens and of the vitreous body dimples and finally invaginates it in front much as the pressure of the finger would a ball of thin rubber, so that in its completed form it is a two-layered cup with its lip at the pupillary border. (See page 176 and Fig. 59.)

The outer layer retains, throughout, its primitive epithelial character, becoming strongly pigmented. Its close apposition to the middle coat and its ready separation from the inner layer caused it to be formerly incorrectly reckoned as belonging to that coat, although it is now known to be genetically distinct. The inner layer is variously modified in the different regions which it traverses. Behind, where it is fully nourished by the chorioid, it has become strongly developed; in the ciliary region, where the nourishment is less, it retains its embryonic condition; while in front, where it lines the iris, it has become reduced to a mere epithelial investment. There are, therefore, three portions of the coat showing successive degrees of reduction: first, the retina proper or chorioidal retina, extending from the optic nerve entrance to the ora serrata; second, the ciliary retina, extending from the ora serrata to the iris; third, the iridian retina, forming the posterior layers of the iris. The latter has already been described with the iris.

FIG. 59.



Model showing formation of optic cup. (Bonnet.)—*Sn*, optic nerve or hollow pedicle of the cup, enlarged forward into a vesicle with an outer wall (*ab*), an inner wall (*ib*), and a cavity (*h*), which later disappears. The furrow (*aus*) on the lower side of the stalk is the chorioid fissure, which farther forward is filled in with the vitreous body (*gl*) and the lens (*l*).

THE RETINA PROPER.[2]

The inner layer of this portion of the nervous coat is conterminous with the chorioid portion of the middle coat, and is characterized, except where the fibres of the optic nerve enter, by a complicated arrangement of cellular layers which constitute the receiving apparatus for vibrations of light. It extends from the optic nerve entrance on the posterior two-thirds of the globe, a little farther forward on the medial than on the lateral aspect, ending at the wavy line called the ora serrata, by losing its essential nervous elements.

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[1] That the seat of vision is in the retina has by no means been universally held by investigators. Mariotte, Méry, Le Cat, and Sir David Brewster were of the opinion that the chorioid is the active agent in perception. In 1793, John Taylor published a treatise entitled "An Important Inquiry into the Seat of the Immediate Organ of Sight,—viz., whether Retina or Choroides."

[2] Syn.: *pars optica retinæ;* physiological retina; chorioidal retina.

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It gradually decreases from a thickness of 0.4 millimetre behind to about 0.2 millimetre near the ora serrata. In health it is perfectly smooth, being well stretched over the chorioid, but after death it rapidly swells up by imbibition, so that folds appear, usually directed meridionally. Its transparency is so great that during health it can be distinguished only by its blood-vessels, which seem to float within it, or, after it has been for a time deprived of light, by a purplish-red tinge due to a disseminated coloring matter termed the visual purple. Hence in the interior of the eye the outer or pigmented layer shows through the inner transparent layer, forming a dark background which prevents reflection of the rays of light and consequent interference. Immediately after death the retina becomes clouded, then appearing as a thin grayish pellicle. In a short time it grows soft and diffluent. Pathological causes may also change its transparency during life, and its examination by means of the ophthalmoscope gives us important information as to its blood-vessels and the general nutrition of the tissues.

The general transparency of the retina is, however, obscured in two places,—one, where the optic nerve enters, called the optic disk; the other, an elliptical area lying in the ocular axis, called the yellow spot.

The *optic disk*[1] is a whitish spot opposite the attachment of the optic nerve, composed of the fibres of that nerve that have penetrated the lamina cribrosa and are bending at nearly right angles to diverge meridionally to all parts of the retina. (See Fig. 60.) It appears to be circular, or nearly so, but accurate measurements show it to be slightly elliptical, with its long axis directed vertically. Its diameters vary from 1.4 to 1.7 millimetres. The divergence of the fibres causes its surface to be depressed in a varying degree; sometimes it is a mere dimple, or it may be deepened to a considerable funnel-like hollow, the *excavation*.[2] This is not situated at the centre of the disk, but somewhat towards its nasal side, where the wall of the excavation is somewhat steeper and the retinal vessels are found, they having penetrated at the bottom of the funnel. The passage by which they penetrate is known as the *porus opticus*, a name erroneously applied by some to the entire disk. It may be noted that the excavation is the natural result of the invagination of the optic vesicle in the embryo, and should be considered as a vestige of the chorioidal fissure. A vestige of the hyaloid

[1] Syn.: *porus opticus; colliculus opticus; papilla optica;* optic papilla; optic entrance; head of the optic nerve; *punctum cœcum;* blind spot; Mariotte's spot (discovered as to this property by Mariotte in 1668); *macula albida*, Luschka. The designations *papilla* and *colliculus* were used by the older anatomists for the reason that when viewed in a fresh eye the disk appears elevated. This is, however, an optical illusion produced by the whitish nerve-fibres showing through the transparent surroundings. There is really no elevation of the disk as a whole, but, on the contrary, a slight excavation. For this reason the term optic disk is to be preferred.

[2] Syn.: *excavatio papillæ nervi optici; excavatio physiologica;* physiological excavation. The latter names contrast it with the much larger pathological excavation involving the whole disk that at times results from a considerable increase of intra-ocular pressure.

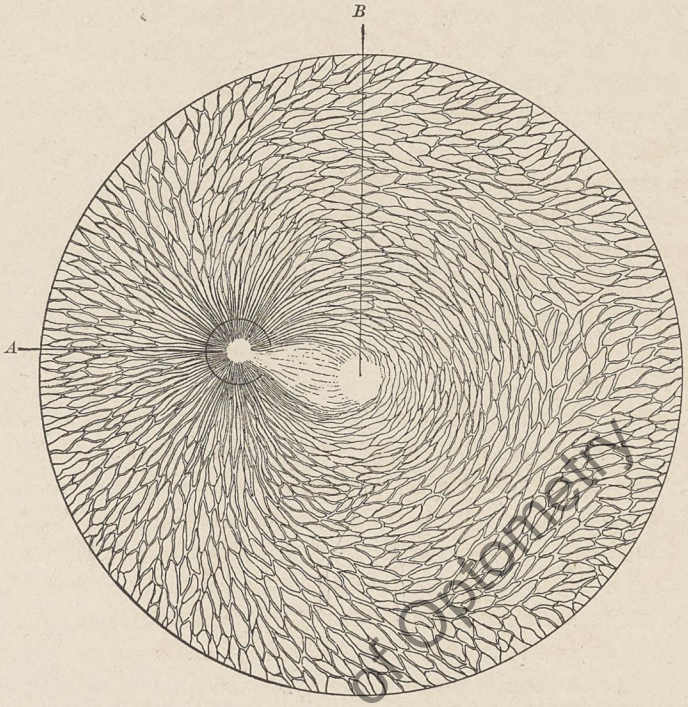
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artery of fœtal life may often be found here, appearing as a thread of connective tissue running from the disk into the vitreous body.

The whitish appearance of the disk is due to the fact that the lamina cribrosa and the myelinated fibres beyond it show through the transparent axis-cylinders which alone form the disk. The proper perceptive elements of the retina are here entirely absent.

Viewed through the ophthalmoscope (see Fig. 61), the disk presents some appearances that depend upon its structure. Immediately surrounding it there is usually seen a whitish circle, the *scleral ring*, it being an

FIG. 60.



Radiation of the optic nerve fibres upon the retina. (Michel.)—*A*, optic disk; *B*, macula lutea. The image is reversed.

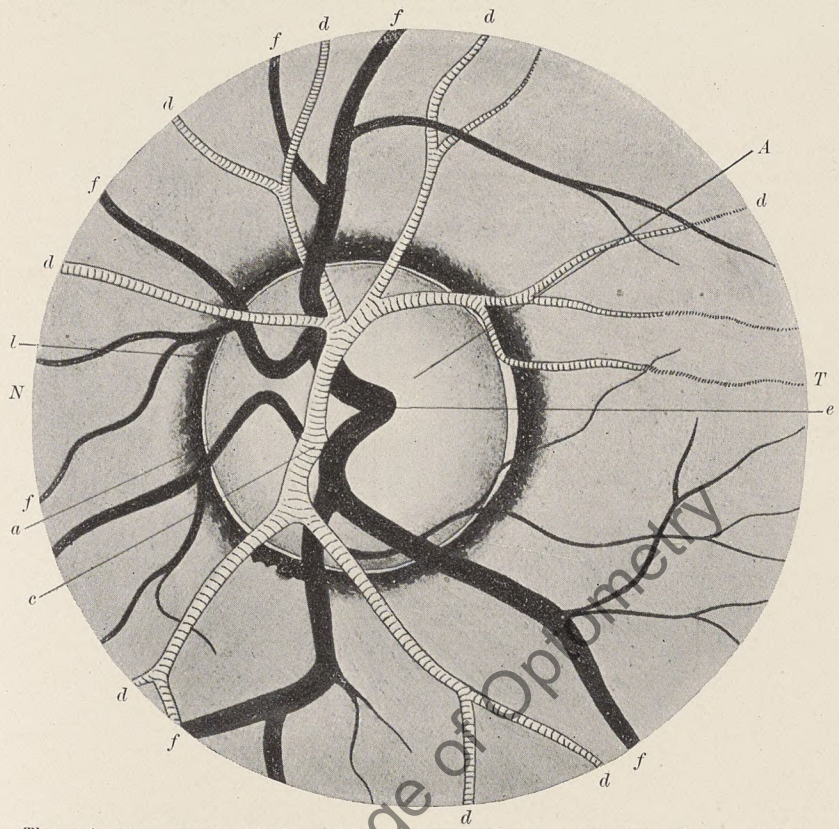
edge of sclera that shows through the somewhat larger chorioidal aperture. Exterior to this there is often seen a dark circle, the *chorioidal ring*, frequently broken by the passage of vessels so as to form two or more crescents. This is due to the showing of the pigment of the chorioid, often especially well developed in this locality. Within this a fine reddish-gray line indicates the proper edge of the nerve. These rings are somewhat obscured on the nasal side because there a greater number of fibres pass over them.

The *yellow spot*[1] is an oval area of a reddish-brown color that appears

[1] Syn.: *macula lutea; limbus luteus*, Sömmering. It was first discovered by Bozzi, not by Sömmering, as is usually stated.

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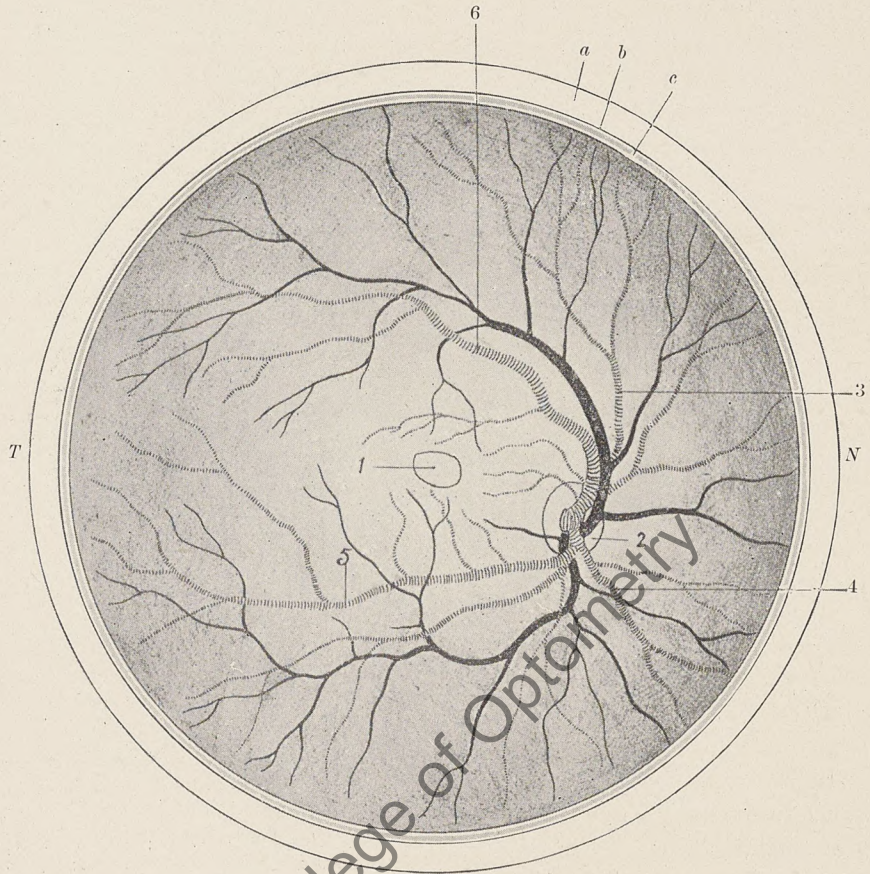
FIG. 61.



The optic disk viewed with the ophthalmoscope. (Jäger.)—*A*, the optic disk; *a*, scleral ring; *b*, chorioidal ring; *c*, central artery of retina; *d*, *d*, its branches; *e*, central vein of retina; *f*, *f*, its branches; *N*, nasal side; *T*, temporal side.

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FIG. 62.



Vessels of the retina. (Testut.)—*a*, sclera; *b*, chorioid; *c*, retina; 1, macula lutea; 2, optic disk; 3, superior nasal artery; 4, inferior nasal artery; 5, inferior temporal artery; 6, superior temporal artery; *T*, temporal side; *N*, nasal side.

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somewhat darker than the rest of the retina because of pigment granules diffused throughout its tissue. Its horizontal diameter is about two millimetres, and its vertical diameter half that distance. This, however, can be determined only approximately, because the coloring-matter fades away gradually. In the retina which has been removed from the chorioid it is of a golden-yellow hue. The color soon disappears after death, probably dissolved by extravasated fluids.

Near the centre of the yellow spot there occurs a funnel-shaped depression known as the *central fovea.*[1] This is situated nearly in the axis of the globe at an average distance of 3.915 millimetres[2] from the centre of the optic disk and 0.785 millimetre below the horizontal meridian (Landolt), a distance which varies according to the shape of the ball, being greater in hypermetropes and less in myopes. It is the region of most acute vision, and it is because of the localized character of this acuity that the eye must be moved when scanning carefully a surface of any extent. Its diameter is from 0.2 to 0.4 millimetre,[3] and it is so deep that the retina at its bottom or fundus is thinner than at any other place, being only 0.1 to 0.08 millimetre thick. With the ophthalmoscope it can usually be discerned as a clear speck situated in the darker area of the yellow spot.

In retinas examined any considerable time after death a small fold, the *plica centralis,* is seen running from the disk to the macula lutea. This was formerly thought to be an anatomical feature of the living eye, but is now known to be a post-mortem phenomenon.

The vessels of the retina (see Fig. 62) form a system distinct and independent from that of the chorioid, communicating with the latter only at the optic nerve head by means of small twigs that join the circlet of Zinn.

The pathological consequences of this may be readily deduced; the integrity of the central artery is necessary to the preservation of the sight; should it at any time become occluded or compressed, vision at once fails for lack of retinal nutrition. Besides, the retinal arteries do not anastomose with one another, every arteriole supplying its appropriate area and terminating in its own capillaries. In this respect the vessels behave very much like those supplying the cortex of the brain. (See Fig. 63.) From this method of termination, quite distinct from the ordinary distribution, such vessels are called *terminal arterioles.* In case any branch is plugged, the area it supplies is at once deprived of a proper circulation, and loss of vision at once ensues there.

The trunk artery of the retinal system is the central artery of the

---

[1] Syn.: *fovea centralis; foveola centralis; Netzhautgrube,* G.; *foramen centrale,* Sömmering. The retina being very thin here, the subjacent pigment shows through very distinctly, even after the tissue becomes clouded after death. The fovea then appears as a clear punctiform spot, and was at first supposed to be a foramen.

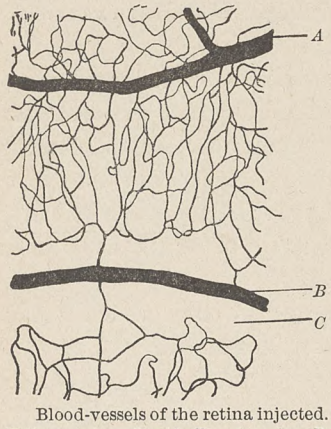
[2] 3.88 millimetres, Schäfer; 3.8 millimetres, Weber; 3.28 to 3.6 millimetres, Krause; 4 millimetres, Gerlach and Macalister.

[3] 0.18 to 0.225 millimetre, Kölliker.

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retina, a branch of the ophthalmic, which in the fœtus supplies the anterior part of the primitive optic vesicle, and becomes enfolded in the optic nerve when the invagination of that vesicle forms the optic cup. It enters the nerve some 1.5 centimetres behind the eyeball, and runs within it as far as the fundus of the excavation of the disk. Within this excavation it usually divides into two principal branches, the superior and inferior papillary arteries. Each of these soon divides into a temporal and a nasal branch: so that there are four principal arteries supplying the four principal aspects of the retina,—viz., the superior and inferior temporal and the superior and inferior frontal arteries. It should be noted that, owing to the situation of the optic disk in the inferior nasal quadrant, the artery for that quadrant has much less area to supply than the others, while the superior temporal artery has much more than the others; the former is consequently the smallest, the latter the largest, of these branches. Some small twigs given off from the papillary arteries pass towards the region of the yellow spot, and are designated as the superior and inferior macular arteries. Others pass towards the median line, and are called the median arteries.

FIG. 63.



Blood-vessels of the retina injected. (Böhm and v. Davidoff.)—*A*, vein; *B*, artery; *C*, free area near artery.

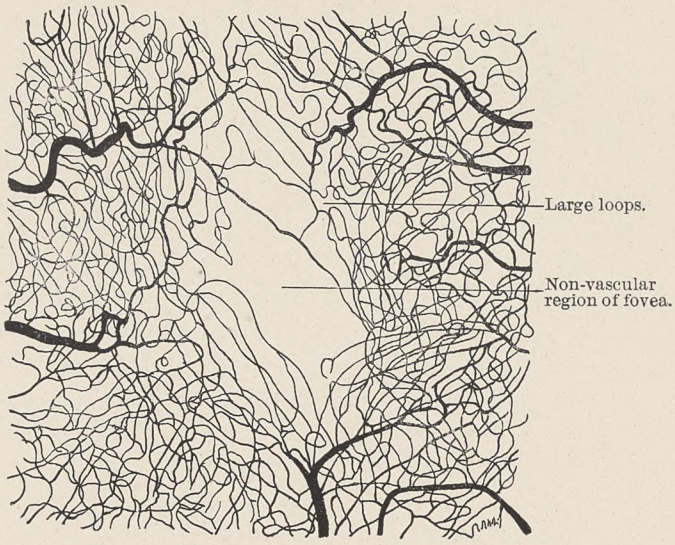
The main branches of the retinal system run in the deeper layers of the retina, sending vertical offshoots to supply the immediately contiguous layers. The most superficial layers are not supplied from that system, their nutrition depending upon transudation from the choroidal vessels, as has already been explained. This lack of blood-vessels in the external layers explains why none are found in the immediate region of the central fovea. The retina is reduced at that place to its outer layers, and there is consequently an area of about one-sixth of a square millimetre that is entirely destitute of blood-supply. The region of the yellow spot is, however, one of the best supplied of the whole retina, it receiving a multitude of fine twigs from both the temporal and macular arteries (see Fig. 64): so there is every reason to think that its nutrition is especially active.

The capillary vessels are arranged in an internal, large-meshed network and an external, much finer one. From these arise the veins, that follow courses corresponding inversely to those of the arteries and discharge into the cavernous sinus or the superior ophthalmic vein.

Numerous variations of the distribution of the retinal arteries have been found, depending upon the place at which the central artery divides. This division may occur at the margin of the disk, immediately at the exit of the artery from the nerve (normal form), or within the trunk of the nerve (quite frequent), and the arteries may indeed again subdivide into

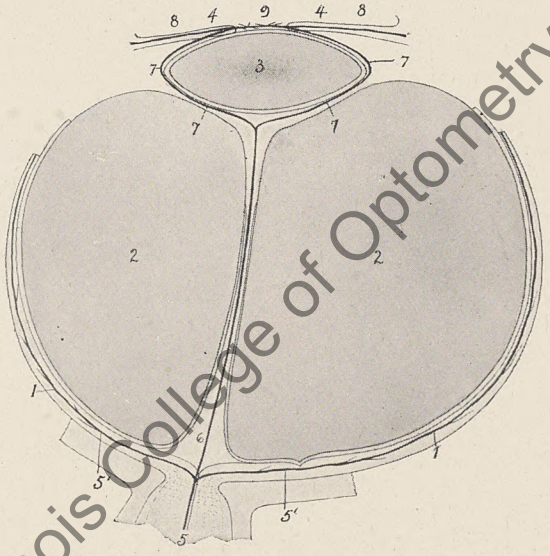
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FIG. 64.



Blood-vessels of the yellow spot injected. (Böhm and v. Davidoff.)

FIG. 65.



The hyaloid artery. (Testut.)—1, retina with its vessels; 2, vitreous body; 3, crystalline lens; 4, iris; 5, central artery of the retina, with 5′, 5′, its branches; 6, hyaloid artery; 7, 7, its branches supplying the posterior surface of the lens; 8, 8, iridian arteries; 9, anastomosis of the two systems upon the capsulo-pupillary membrane.

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nasal and temporal branches within the nerve, and appear upon the disk as four trunks.[1]

During fœtal life the retinal system supplies the contents of the optic cup as well as the cup itself. A vessel passes from the central artery at the disk forward through the vitreous body and supplies the vascular tunic of the lens. (See Fig. 65.) This—the *hyaloid* artery—may persist to adult life and offer no serious obstacle to vision. The connection of this vessel with the arteries of the iris has already been mentioned.

The layers of the retina are fully considered in the article that treats of its microscopical anatomy. It is only necessary to state here that the outer layer of the optic cup forms a sheet of densely pigmented epithelium, while the inner one is differentiated into neuro-epithelial elements, constituting the visual cells, or rods and cones, and the neural elements proper. There is also a system of supporting fibres, probably of the nature of neuroglia, known as Müller's fibres. The arrangement of the nerve-cells is not unlike that of those found in the cortex of the brain, there being evidently receiving, associative, and transmitting elements, as well as filaments apparently derived from the central organs that seem to represent afferent fibres.

At the region of the yellow spot the inner layers thin away and become reduced until at the central fovea the neuro-epithelium alone remains.

THE CILIARY RETINA.[2]

At the ora serrata the nervous elements of the retina suddenly cease, and there remain only the external, pigmented epithelium and an undifferentiated, internal layer representing the primitive condition of the optic vesicle. This portion of the retina is reduced in thickness to 0.2 millimetre. It is continuous forward with the posterior pigmented epithelium of the iris. The width of this region—that is to say, the distance from the ora serrata to the attachment of the iris—is five millimetres.

CONTENTS OF THE EYEBALL.

Within the coats just described are contained certain transparent media. These were formerly known as the *humors of the eye*, and were distinguished, according to their characters, as the aqueous, crystalline, and vitreous humors,—the first being liquid and watery, the second a soft solid having a definite structure, and the third having a jelly-like consistency. With the decline of the doctrine of the humors these names have been gradually abandoned, the first only being retained, the crystalline humor being known as the *crystalline lens*, and the vitreous humor as the *vitreous body*.

The three have a diversity of origin: the aqueous humor is a secretion derived from the blood, especially through the ciliary processes; the lens

[1] See Magnus, Die makroskopische Gefässe der menschlichen Netzhaut, Leipzig, 1873.

[2] Syn.: *pars ciliaris retinæ; corpus ciliaris retinæ; margo flocculosus retinæ;* pre-retina (Leidy).

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is an ectodermic invagination; while the vitreous body is of mesodermic origin, being an excellent example of a mesenchymal structure.

THE AQUEOUS HUMOR.[1]

This is a sparkling, transparent lymph filling the aqueous chamber or space in front of the lens, which is morphologically a lymph-space. As already stated, it is separated from the blood by the action of the vessels of the middle coat, particularly those of the ciliary processes. It was formerly believed to be essential to vision and fixed in its quantity, so that if evacuated it was not renewed and blindness necessarily ensued. Zinn[2] showed this not to be the case.

Many theories have at various times been brought forward to account for its production. Palfin supposed that he had discovered special glands for its secretion at the edge of the iris; Nuck indicated special conduits for its transmission, which were, however, shown to be the long anterior ciliary arteries. Some have supposed that it was an oozing from the vitreous body,—that it was the secretion of a special membrane, the mythical aqueo-capsulary membrane, believed to line the entire surface of the aqueous chamber. The view of Collins, that it is mainly secreted by certain gland-like bodies found upon the surface of the ciliary processes, has been already mentioned. The older view of Méry,[3] that the ciliary processes throughout their whole extent are the agents of the secretion, seems to be the correct one. With these should probably be included the vascular ridges that extend from the ciliary processes to the posterior surface of the iris. It is pointed out by Leber that the tubular invaginations of Collins have not the anatomical character of glands, as they have no secretory duct, no proper lumen, and no glandular epithelium. Nicati[4] endeavors to show that in addition to the ciliary processes the choroid itself must be considered as a secreting organ for this liquid, of which he distinguishes two kinds,—one, non-fibrinous or ordinary, which occupies the chambers when no pathological conditions are present; the second, fibrinous or neuro-paralytic, secreted during pathological conditions, such as a sudden evacuation of the chambers, or special affections of the sympathetic nerve. In opposition to this view, Leber[5] remarks that there is no anatomical structure

[1] From L. *aqueus*, *-a*, *-um*, watery, and *humor* (or *umor*), fluid, moisture.
Syn.: *humor aqueus*; *Wasserfeuchtigkeit*, G.

[2] "Secernitur et renovatur ut ex notissimis et plurimis illis observationibus apparet, quibus constat, humorem aqueum, qui per vulnusculum corneæ inflictum effluxit, ut oculus collaboretur, intra quadraginta et octo horas, perfecte renasci et oculum illo, ut antea repletum inveniri." Zinn, Descriptio oculi humani, Gottingae, 1755, chap. vi. §§ 2, 3.

[3] Méry. Scavoir si le glaucoma et la cataracte sont deux différentes ou une seule et même maladie. Mém. de l'académie des sciences, 1707, p. 498.

[4] Nicati. La glande de l'humeur aqueuse. Archives d'ophtalmologie, Paris, 1890, x. 481, and 1891, xi. 24, 152.

[5] Leber (Th.). Der gegenwärtiger Stand unserer Kenntnisse vom Flüssigskeitswechsel des Auges. Ergebnisse der Anatomie und Entwickelungsgeschichte, 1894, Bd. iv., Wiesbaden, 1895.

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behind the ciliary processes that could serve as a secretory organ. Nicati apparently overlooked the fact that the chorio-capillary layer of the middle coat does not extend forward of the ora serrata.

The importance of these investigations is very considerable, as it is almost certain that glaucoma is dependent in some way upon the production of this fluid.

When the chamber is evacuated the secretion is quite rapid, refilling the cavity in a few moments. It does not seem, however, that under ordinary normal conditions there can be any very rapid production of the fluid, for if the normal interocular pressure is maintained after puncture there is no sensible increase in the fluid. That some production is constantly going on appears clear from the fact that after death the interocular pressure decreases gradually, which would not be the case were it dependent merely upon vascular tension.

Those who hold that other portions than the ciliary processes assist in this production note that the fluid is freely secreted before the pupillary membrane is obliterated,—that is to say, while the anterior and posterior chambers are still separated from each other. On the other hand, it is stated that the anterior chamber is not formed until the pupillary membrane begins to disappear, and that the slightest break in the continuity of the latter would necessarily fill the newly developed lymph-space. Again, the humor is said to be found in normal quantity after inflammations which occasion a complete adhesion of the iris to the lens, shutting off the ciliary processes. This, however, is by no means conclusive, as there is nothing to show that the fluid which certainly existed in the anterior chamber before the adhesion occurred has been absorbed. That it is more freely formed in the posterior chamber is shown by the fact that when posterior adhesions of the iris exist, a forward bulging of that organ occurs, indicating a collection of fluid behind it. The experiments of Deutschmann[1] show that extirpation of the ciliary body is followed by a complete cessation in the production of the aqueous humor; indeed that in a short time the vitreous humor also is absorbed, so that there remains little else than the crystalline lens within the contracted eyeball. Whether such extensive interference with the anatomical structure of the organ as is necessary for the complete removal of the ciliary body can be effected without involving the relations and functions of other parts seems open to question. The humor leaves the chamber by the spongy tissue of the spaces of Fontana, as already described in speaking of the sinus venosus. It also passes out by the lymph-crypts of the iris. The lowering of the intra-ocular tension which necessarily occurs when the humor is evacuated causes the blood to pour in increased quantity into the iris and the ciliary body, which greatly aids the transudation of fluid.

[1] Deutschmann (R.). Ueber die Quellen des Humor Aqueus im Auge. Archiv f. Ophthalm., 1880, xxvi., Abth. iii., 117–134.

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The tension of the eyeball is kept up mainly by the active secretion of the aqueous humor, and, as this tension amounts to the force exerted by a column of mercury twenty-six millimetres in height, it is not surprising that when the cornea is punctured the fluid should rush with some force towards the avenue of escape. This rush is, in fact, so great that it sweeps the iris with it: hence great care must be taken in operating upon the cornea to prevent the iris from being carried into the lips of the wound and becoming fixed there.

According to Nicati, the liquid of the anterior chamber is never quiescent, but has an incessant rotary movement which prevents any deposits from being formed on the surfaces of the chamber.

The aqueous humor is an active agent in removing material from the eye. Blood diffused into the anterior chamber may be seen to disappear in the course of a few days, being dissolved in the aqueous humor and then absorbed. It has also a solvent power for other organic substances, such as the substance of the crystalline lens. If the capsule of the lens be wounded so as to permit the access of the aqueous humor to it, the lens will be gradually absorbed and in favorable cases disappear entirely. This is taken advantage of in operating for cataract by the process of discission.

The index of refraction of the aqueous humor is of value in considering the optical properties of the eye. It is variously stated by different authorities as follows:

Observer.	Index of Aqueous Humor.	Index of Distilled Water.
Chossat[1]	1.338	13358
Brewster[2]	1.3366	13358
W. Krause[3]	1.3420	13342
Helmholtz[4]	1.3365	13354
Fleischer[5]	1.3373	13340
Hirschberg[6]	1.3375	

Krause found that in the eyes of calves the refractive indices were not materially changed within twenty-four hours after death.

The quantity of the aqueous humor in the eye is not great, being but from two hundred and thirty-one to three hundred and twenty-three cubic millimetres. Its weight is from 0.233 to 0.325 gramme, and its specific gravity is nearly that of water, being 1.0053.[7]

The latest determinations of its chemical composition are those of Michel and Henry Wagner,[8] who experimented on swine, finding the following:

[1] Bulletins de la Société philomathique de Paris, 1818, p. 95.

[2] Edinburgh Philosophical Journal, 1819, i. 43.

[3] Die Brechungsindices des menschlichen Auges. Hannover, 1855.

[4] Handbuch der physiologischen Optik, 1867, S. 78.

[5] Neue Bestimmungen der Brechungsexponenten der durchsichtigen flüssigen Medien des Auges, 1872.

[6] Centralblatt für die medicinischen Wissenschaften, 1874, xii. 193.

[7] These figures are from Vierordt, Daten und Tabellen, 1893.

[8] Archiv für Ophthalmologie, 1886, xxxii., Abth. ii., 155.

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	Per Cent.
Water	98.71
Ash	0.89
Albumin	.107
Other organic substances	.293
	100.

The extraordinary solvent power of the aqueous humor makes it easily affected by drugs circulating in the blood. One of the tests for poisoning by belladonna or atropine is to drop a little of the aqueous humor from the eye of the suspected subject into the eye of another animal. If atropine is present, dilatation of the pupil of that animal soon ensues. Some drugs color the humor sufficiently to affect vision. This is the case with santonin, even in medicinal doses, the patient often "seeing yellow" for some hours after taking it.

THE CRYSTALLINE LENS.[1]

This was early recognized as one of the most important of the accessory structures of the eye, its optical properties being described by Kepler, Descartes, and other early writers upon vision. Maurolycus[2] appears to have been the first to compare it to a lens of glass, and to affirm that it had the power of refracting rays of light.

Scheiner[3] was the first to demonstrate its function, and to prove that the rays are focussed upon the retina. This he did by stripping away the sclera behind and allowing a beam of light to pass through the eye and fall upon a screen.

Possessing, as it does, the property, unique among optical apparatus, of changing its form for the purpose of producing greater or less refraction of the rays of light, it was thought by Leeuwenhoek to be of a muscular character, and he accordingly named it the *musculus crystallinus*.

It is, as its name implies, a transparent lenticular body, biconvex in shape, with a circular margin, situated between the aqueous and vitreous chambers, touching the iris on the one side and the vitreous body on the other, its anterior surface being applied to the pupillary orifice, and its posterior surface fitting into a saucer-shaped depression of the vitreous. It is surrounded and held in place by a suspensory apparatus known as the zonula, derived from the hyaloid membrane of the vitreous body. The distance of its rounded edge from the ciliary processes is from 0.5 to 0.6 millimetre.

Its anterior pole is distant from the cornea about 2.3 millimetres, and its posterior pole from the yellow spot 15.6 millimetres. For rough estima-

[1] From L. *lens, lentis*, a lentil, in allusion to its biconvex shape.

Syn.: *lens crystallina; humor crystallinus; corpus crystallinum; cristallin*, F.; *Linse, Krystalllinse*, G. Some of the older anatomists called it *gutta*, from the expression of Celsus, "gutta humoris, ovi albo similis." Hence those cases of amaurosis in which the lens is not affected were called *gutta serena*. (Hyrtl.)

[2] Fr. Maurolyci. Photismi de lumine et umbra ad perspectivam et radiorum incidentiam facientes. Venetiis, 1575.

[3] Scheiner (C.). Oculus, sive fundamentum opticum. Œniponti [Innspruck], 1619.

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tions it may be stated that its posterior pole is nearly at the junction of the anterior and middle thirds of the optical axis.

Tscherning[1] has shown that the antero-posterior axis of the lens does not correspond exactly to the axis of the eye, the deviation being such as would occur if the structure had been rotated around a vertical axis outwardly from three to seven degrees. A slight rotation may also be observed in some cases around a transverse or frontal axis, the deviation here ranging between zero and three degrees.

In order to remove the lens for examination it is necessary to cut away the cornea, raise the iris, and carefully snip with small blunt scissors the suspensory ligament around its whole circumference. It can then be lifted out, care being taken to detach any adherences that may exist between it and the vitreous body.

The lens is about nine millimetres in its transverse diameter, varying in size somewhat with age and stature, being larger in the old and in very tall persons. Its antero-posterior diameter, or thickness, varies according as it is accommodated for near or for distant vision, as do also the curvatures of the anterior and posterior surfaces. Practically these may be stated in round numbers as follows:

	Distant Vision. Millimetres.	Near Vision. Millimetres.
Thickness	3.7	4
Anterior radius	10.	6
Posterior radius	6.	5

In distant vision the anterior radius is to the posterior about in the proportion of three to two. Since the invention of the ophthalmometer more minute measurements have been attempted. The following are those of Woinow,[2] and are probably the most accurate:

	Accommodated for	
	Distant Objects.	Near Objects.
Thickness	3.0247–3.96269	3.5129– 4.4784
Radius of anterior surface in young persons	8.9452–10.2091	5.1466– 6.8507
Radius of anterior surface in old persons	9.1139–12.5804	7.3104–10.1731
Radius of posterior surface in young persons	6.248– 7.1905	4.9714– 6.2817
Radius of posterior surface in old persons	6.06353– 8.0013	4.6941– 6.3792

It will be seen, therefore, that the curvature of the anterior surface is much more affected than that of the posterior by the action of the ciliary muscle. It should be remembered that the action of that muscle, by withdrawing the tension of the suspensory ligament, allows the lens to assume its own unmodified shape. The length of a meridian is about twelve millimetres.

[1] Tscherning. Sur la position du cristallin de l'œil humain. Comptes rendus hebdomadaires des séances de l'Académie des Sciences, Paris, 1888.

[2] Woinow (M.) Ophthalmometrie. Wien, 1871.

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Attempts have been made to classify the curved surfaces of the lens under some regular form. Kepler thought the anterior surface to be that of a spheroid, the posterior that of a hyperboloid. Chossat, Vallée, and Krause considered both surfaces as ellipsoidal, formed by the revolution of an ellipse about its minor axis. Brücke believed the anterior surface to be ellipsoidal, and the posterior paraboloidal. It is probable that neither curvature is perfectly regular.

The weight of the lens, as determined by Sappey[1] from eleven specimens, is from .20 to .25 gramme, the lowest weighing .201 gramme, the highest .252 gramme, the average being .218 gramme. The weight increases slightly with age, which may account for the estimations given by Vierordt,[2] who states the weight of the lens as ranging from .28 to .29 gramme.

Its specific gravity is greater than that of either the aqueous or the vitreous humor, being stated by Nunneley[3] as 1121. Consequently, whenever the lens is displaced by the rupture of the suspensory ligament it falls to the bottom of the eyeball.

Monoyer[4] gives its volume as one-fourth of a cubic centimetre.

The lens is so nearly transparent that in early life it appears to have no color, or, if any, a very slight bluish tinge, when it is seen by oblique illumination. With advance of years it assumes a yellowish hue, or may present a slight trace of opalescence, this latter being one of the causes which occasion the slight grayish or grayish-green dimness that appears in the pupils of aged people when compared with the intense black of youth. The coloration affects first the central portion of the lens, and gradually extends to the cortical part. In some cases it may be sufficient to affect the appreciation of colors. It is said of the painter Mulready that in all the compositions executed by him during the later years of his life he had a false scale of color, which greatly reduced the yellow tints and increased the blue ones, so that in order to judge properly of his works it is necessary to view them through a glass slightly tinted with yellow.

When exposed to the air the lens becomes dulled in lustre and slightly wrinkled, and also loses a portion of its transparency. Immersed in water it swells, becomes milky, and bursts its capsule, which, after letting out a small amount of opaline fluid, again contracts closely upon it. All agents that coagulate albumin, such as silver nitrate, gold chloride, osmic acid, etc., harden it.

When pressed between the fingers or by a blunt instrument the lens readily changes its figure, springing back to its original shape as soon as the pressure is removed. In fact, it behaves like a soft material enclosed

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[1] Traité d'anatomie descriptive.

[2] Vierordt. Daten und Tabellen für Mediziner, S. 106.

[3] Nunneley, in the Quarterly Journal of Microscopical Science, 1858, p. 138. Davy (Transactions of the Medico-Chirurgical Society of Edinburgh, 1829, iii. 436) states the specific gravity as 1.100, and Chenevix (Annales de chimie, xlviii. 74) fixes it at 1079.

[4] Nouveau dictionnaire de médecine et chirurgie pratique. Paris, 1869, x 259.

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in an elastic envelope. It is easy to demonstrate that this is really the case by slightly staining the envelope with dilute osmic acid, immersing it in water, and scratching it open with a small instrument, when the substance of the lens will peel out, leaving the external envelope or *capsule*[1]—a delicate, shell-like membrane—floating on the water.

It can be easily seen by the unassisted vision that this membrane is thicker in front than behind, and that the two parts meet at a rounded edge, the equator of the lens. The anterior portion is somewhat more than twice as thick as the posterior part, and consequently is more prone to take on pathological changes. This difference in the two parts has led anatomists to apply to them the names of *anterior capsule*[2] and *posterior capsule*.[3] These names are not to be commended, as they seem to imply that there are two distinct investments, when in fact there is no clear demarcation between the two.

The elasticity and strength of the capsule are considerable. It is also very brittle, and if scratched or cut by a sharp instrument readily tears, breaking like thin glass along irregular angular lines, that are usually perpendicular to the surface. This has led some writers to describe the capsule as the *vitreous membrane*. Its cut edges always roll outward, so that the outer surface lies innermost in the roll, behaving in this respect like the internal limiting layer of the cornea, with which, indeed, it presents many analogies. It is entirely structureless, but is readily permeable by coloring matters. Near the equator of the lens the zonula or suspensory ligament is attached, there being no visible line of union. The capsule is remarkably resistant to reagents, as it still retains its transparency after treatment with boiling water, acids, and alcohol. It also resists putrefactive changes for a considerable time. Bowman has pointed out that during life its immunity from change is by no means very great, any injury to the capsule being almost certainly followed by an opacity. Special operative precautions are necessary to prevent its forming an obstruction to light after the removal of the substance of the lens in the needle operation for cataract.

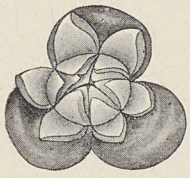
It is well known that the substance of the lens is developed by an invagination of the ectoderm, and that it may, therefore, be considered as epithelial in character. The capsule, however, is probably of mesodermic origin. This matter is more fully discussed in the chapters on the development and the microscopical anatomy of the eye.

The main body of the lens is of a much less firm consistency than the capsule. At an early age this consistency is nearly the same throughout the whole substance, but in advanced years there is a difference between the deeper or more central portions of the lens and those at its exterior. There is no abrupt transition between these parts, and the condensation appears to be due entirely to the absence of metabolic changes in the interior. As

[1] Syn.: *capsula lentis.*
[2] Syn.: *cristalloïde antérieure*, F.
[3] Syn.: *cristalloïde postérieure*, F.

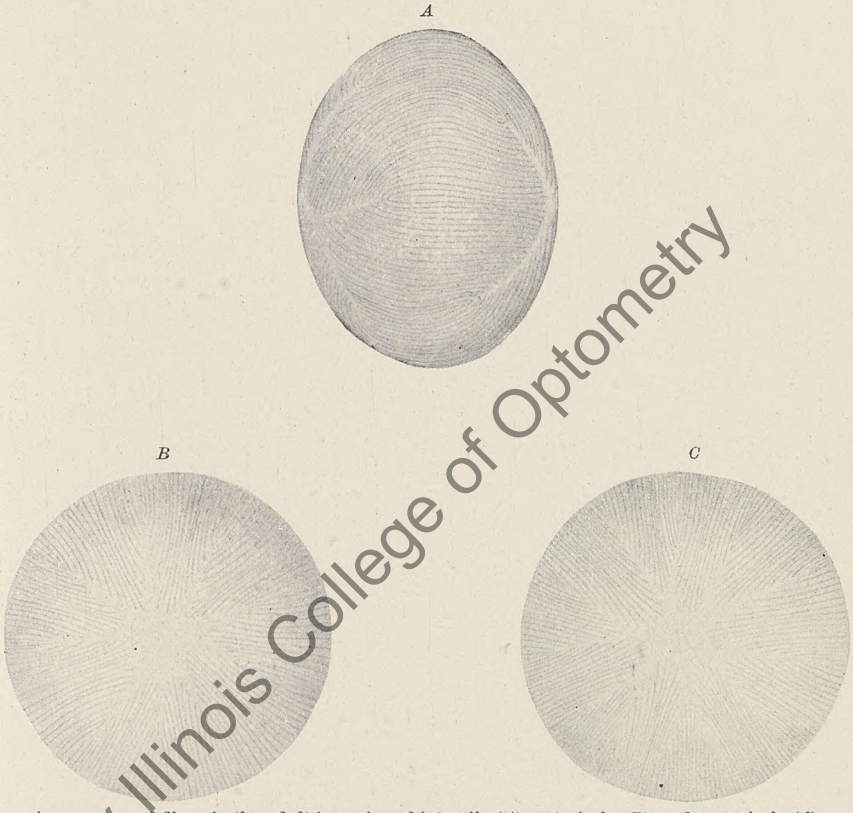
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FIG. 66.



Concentric layers of lens-stars.

FIG. 67.



Appearance of fibres in the adult lens viewed laterally (*A*), anteriorly (*B*), and posteriorly (*C*).

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the adult lens has no blood-vessels, it is nourished entirely by intercellular transmission of fluids, and the condensing process consists mainly in a loss of water. This hardening commences in childhood, but it is not until adult years that a well-marked nucleus can be distinguished. In old age almost the entire lens becomes condensed, so that any alterations in its form are much more difficult. Hence arises the defect in the power of accommodation so well marked in the eyes of persons past middle life. The central condensed portion is usually called the *nucleus*[1] of the lens, while the external softer part is termed the *cortical substance*.[2]

The change in the density of the lens produces other results. For example, as the nucleus reflects more light than the cortical portion, the lens can more readily be seen in the eyes of older people, and the jet black of the pupil is slightly dimmed, as above mentioned. Again, the increased density of the lens affects its power of refracting the rays of light.

The following table shows the refractive power of the lens as determined by different observers :

Observer.	Lens.			Total.	Distilled Water.
	Cortex.	Middle Layer.	Nucleus.		
Young[3]	. . .	. . .	1.4026	1.4385	. . .
Chossat[4]	1.383	1.395	1.420	. . .	1.3358
Brewster[5]	1.3767	1.3786	1.3896	. . .	1.3358
W. Krause[6]	1.4053	1.4294	1.4541	. . .	1.3342
Helmholtz[7]	1.4189	. . .	. . .	1.4467	1.3354
S. Fleischer[8]	. . .	. . .	. . .	1.4371	1.3340
Woinow[9]	1.3968	1.4216	1.4351	1.4387	1.3354
Aubert[10]	1.3967	1.4067	1.4093	. . .	. . .

The following optical constants of the lens were determined by Helmholtz :

	Millimetres.	Millimetres.
Focal length	45.144	47.435
Distance of the first principal point from the anterior surface	2.258	2.810
Distance of the second principal point from the anterior surface	1.546	1.499

[1] Syn.: *nucleus lentis.*

[2] Syn.: *substantia corticalis.*

[3] Philosophical Transactions of the Royal Society of London, 1801, pt. i. p. 23.

[4] Bulletin de la Société philomathique de Paris, 1818, p. 95.

[5] Edinburgh Philosophical Journal, 1819, i. 43.

[6] Die Brechungsindices des menschlichen Auges. Hannover, 1855.

[7] Handbuch der physiologischen Optik, 1867, Ss. 78, 84.

[8] Neue Bestimmungen der Brechungsexponenten der durchsichtigen, flüssigen Medien des Auges. Jena, 1872, S. 26.

[9] Klinische Monatsblätter für Augenheilkunde, 1874, xii. 407.

[10] Gräfe und Sämisch, Handbuch der gesammten Augenheilkunde, 1876, ii. 409.

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After careful consideration of the optical properties of the lens, he concludes:

1. That the focal distances are less than they would be if its entire mass had the index of refraction of its nucleus.

2. The distance which separates the principal points is less in the crystalline lens than in a lens of glass having the same form and whose refracting power is equal to that of the nucleus.

3. A lens having the form of the crystalline lens and the index of refraction of its nucleus would have its principal points distant from each other about one-fourth millimetre.

Some interesting considerations may be raised with regard to the effect on the lens of certain rays at the extremities of the spectrum. It is well known that beyond the limits of vision there are rays of energy extending on the one hand above the violet rays (ultra-violet) and on the other below the red rays (infra-red). The first of these especially effect chemical action, the latter verge towards heat-rays.

Are these rays stopped in any way by the media of the eye, or do they exert an appreciable influence upon the retina?

Certain substances, such as solutions of quinine, guaiacum, etc., have the power of absorbing some of the ultra-violet rays and causing them to appear as a bluish opalescence. This property of these substances is known as fluorescence. It is possessed to some degree by the lens. If resin of guaiacum, properly prepared in the dark, is exposed to diffused light, it appears blue. If, however, the light be passed through the lens of a bullock's eye, the resin appears greenish yellow. This shows that the blue rays are absorbed by the lens.

At the other end of the spectrum it is also found that a considerable number of rays are absorbed. It is well known that glass-blowers, stokers, and others are able to face very intense heat without apparently injuring the eyes. Fritz and Jansen have shown that at least thirteen per cent. of the heat-rays are absorbed by the lens.

It may well be asked whether such a powerful force as this can be arrested by the tissues of the body without producing any marked result. Probably a prolonged exposure to intense heat does lead to degenerative changes in the lens. It is said that cataracts are much more frequently found in persons who have been subjected to such exposure.

Within a short time after death a small amount of fluid appears among the fibres of the lens or between those fibres and the capsule. This fluid, formerly believed to be present during life, and called the *liquor Morgagni*, is now known to be due to post-mortem changes, and is either an infiltration of the aqueous humor or a product of decomposition.

The substance of the lens offers a great contrast to its capsule as regards the effect of physical and chemical reagents. When exposed to the air it rapidly loses its moisture, becomes dry and brittle, and assumes a light straw color. Very cold water causes it to lose its transparency, which is restored

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by placing it in water of the temperature of the air. Boiling water renders it permanently opaque, as do also alcohol and acids.

The structure of the body of the lens will be only briefly referred to here. It is composed of two layers of epithelium lengthened out into long, ribbon-like fibres which are so arranged as to pass from the anterior to the posterior surfaces, leaving on each side certain lines of implantation or dehiscence, the so-called *lens-stars*. When treated by appropriate reagents the lens may be made to cleave along these lines in concentric layers. (See Fig. 66.) The lens-stars, which are different on the anterior and posterior surfaces of the lens, are occasionally sufficiently marked to be observed by the ophthalmoscope or by the subject himself as an entoptic phenomenon. They are simpler in the young than in the adult, giving in front the appearance of a Y turned upside down, behind of the same letter in its erect position. The adult appearance is shown in Fig. 67.

The lens is early to develop. It is at first nearly spherical in form, and does not attain its adult shape until near puberty. Collins[1] found the following measurements in fœtal eyes :

Diameters of Fœtal Eyes and of their Lenses.

Age.	Diameters of Eyeball.			Diameters of Lens.	
	Antero-posterior.	Lateral.	Vertical.	Antero-posterior.	Transverse.
	Millimetres.	Millimetres.	Millimetres.	Millimetres.	Millimetres.
Four months	8.1	7.8	7.5	2.8	3.3
Five months	11.75	11.5	10.5	3.5	4.
Six months	12.5	12.	11.1	3.8	4.5
Seven months	14.3	13.2	12.6	4.	5.
Nine months	16.75	16.	15.3	4.3	5.75
Adult (Merkel)	24.3	23.6	23.4	3.7	9.

From the above it will be seen that during fœtal life the lens is much larger in proportion to the eyeball than it is afterwards. At the fourth month the ciliary processes touch the lens, and it is by the subsequent growth of the various parts that they assume their final position.

It should be remembered that this rapid development of the lens during fœtal life is rendered possible by the nutrition afforded by the net-work of blood-vessels forming the tunica vasculosa lentis already referred to. This disappears at birth or before, and the growth of the lens is thenceforward stationary, it merely changing its shape presumably in accordance with the growth of the other parts of the eye and the various strains to which it is subjected.

What nutritive fluid the lens requires is probably supplied from the ciliary body. It enters the lens near the region of the equator, and circu-

[1] Collins (E. Treacher). Lectures on the Anatomy and Physiology of the Eye, Lancet, London, December 8 and December 22, 1894.

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lates in the interfibrillary clefts. Fuchs cites a case in which a small fragment of iron penetrated the lens, followed by an opacity that assumed a yellowish-green color. Then a circle of rust-colored points appeared corresponding nearly to the margin of the dilated pupil. He believed that the liquid circulating in the lens was removed, and discolored the lens-capsule in this situation.

THE VITREOUS BODY.[1]

The space between the crystalline lens and the retina, constituting about two-thirds of the area of the cavity of the eyeball, is filled with a transparent, watery jelly, enclosed, like the lens, in a delicate capsule. The entire structure is known as the vitreous body. It is by far the largest of the transparent media of the eye. Its shape, almost wholly determined by that of the cavity which contains it, is that of an oblate spheroid, hollowed out in front by a saucer-like depression, the *hyaloid fossa*,[2] into which the lens fits. It is perforated by a central lymph-space, the *hyaloid canal*,[3] that runs somewhat eccentrically from the optic disk to the lens. (See Figs. 3 and 65.)

The mechanical function of this structure is of considerable importance. If for any cause it is permanently decreased in volume, the lens is no longer held firmly in position, but becomes tremulous, and the retina, ceasing to be supported in front, loses its close attachment to the subjacent layers.

The capsule of the vitreous body, called the *hyaloid membrane*,[4] is a very delicate investment in contact behind with the internal limiting membrane of the retina. It is thickened in front, where it forms the suspensory ligament of the lens, and is again thinned to extreme tenuity in the hyaloid fossa. It has no demonstrable structure, and its very existence is denied by many eminent authorities, among whom may be mentioned Henle,[5] Iwanoff,[6] and Merkel.[7] These observers hold that the appearance of a membrane, which is unquestionably present in specimens suitably prepared for microscopical examination, is due to the reagents that are

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[1] From L. *vitreus*, *-a*, *-um*, glassy, alluding to its glassy and hyaline character.

Syn.: *corpus vitreum*; *vitreum*; *humor vitreus*; vitreous humor; vitreous; *corpus hyaloideum*; *Glaskörper*, G. The term vitreous humor is often used for the fluid portion only, as distinguished from the capsule.

[2] Syn.: *fossa hyaloidea*; *fossa patellaris*; *fossa lenticularis*.

[3] Syn.: *canalis hyaloideus*; *canalis Cloqueti*; Cloquet's canal (mentioned by Jules Cloquet, an anatomist of Paris, 1787–1840, in his "Mémoire sur la membrane pupillaire et sur la formation du petit cercle artériel de l'iris," Paris, 1818); *canalis Stillingi*; canal of Stilling (being first fully described by J. Stilling in his article "Zur Theorie des Glaucoms," Archiv f. Ophth., Berlin, 1868, xiv., Abth. iii., 259.

[4] From ὑαλος, glass, and εἶδος, resemblance.

Syn.: *membrana hyaloidea*; *tunica hyaloidea*; *hyaloidea*; *hyaloidea interna*; *tunica arachnoidea*; *membrana vitrea*.

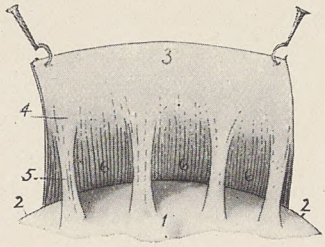
[5] Eingeweidelehre, p. 669.

[6] Stricker's Handbook, American edition, p. 875.

[7] Topographische Anatomie, 1887, i. 266.

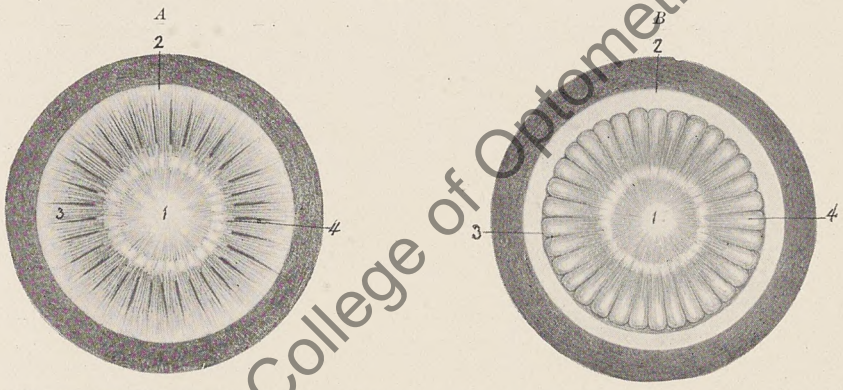
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FIG. 68.



Attachment of the suspensory ligament of the lens. (Testut.)—1, posterior surface of the lens; 2, its equator; 3, the suspensory ligament improperly shown as a continuous membrane; 4, fibres passing forward to the anterior portion of the capsule; 5, fibres passing to the posterior portion of the capsule; 6, 6, the zonular spaces or segments of the canal of Petit.

FIG. 69.



The suspensory ligament of the lens. (Testut.)—*A*, non-injected: *B*, injected: 1, lens; 2, posterior portion of the ligament; 3, anterior portion; 4, its insertion into the lens in *B*, showing the zonular spaces inflated with air.

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necessarily employed in the preparation. As the entire vitreous body may be removed from its chamber and lie as a self-limited mass from which fluid gradually drains away, it seems unreasonable to doubt the existence of this envelope.

Behind, at the optic disk, where the retinal vessels enter, and where in the fœtus the vessels supplying the vitreous body are given off, the hyaloid membrane is somewhat firmly attached. At the ciliary part of the retina also its adhesion is intimate. Along the corona ciliaris, however, while the membrane becomes thicker, it is not so adherent to the adjacent layers. Though intimately attached to the apices of the ciliary processes, it passes over the valleys between those processes with their secondary folds, thus leaving a series of radial spaces that communicate in front with the posterior aqueous chamber and contain aqueous humor. These are known as the *recesses of the posterior chamber*.[1]

Leaving the ciliary processes, the hyaloid membrane is strengthened by the fibres belonging to the *suspensory ligament of the lens*.[2] These fibres do not form a continuous sheet, as was formerly supposed, but leave the neighborhood of the ora serrata in several sets, some of which are inserted on the lens near the equator, others in front, and still others behind it. A more complete description of this arrangement is given in the article on the microscopic anatomy of the eye. The insertion of the fibres is shown in an imperfect manner in Fig. 68. In this figure the suspensory ligament appears as a continuous sheet, which it probably is not, there being many interspaces between the fibres by which fluid can pass between the aqueous and vitreous chambers.

The regularity of the insertion of the fibres about the equator of the lens is such that it is possible with a very fine canula to inject air into a series of spaces between the zonula and the hyaloid membrane, where it remains, showing a series of bullæ. This experiment was first performed by Petit, and he naturally supposed that it demonstrated the existence of a canal extending about the lens in the folds of the suspensory ligament. He named it the *canal godronné*, or ruffed canal, from its similarity in appearance when injected to a certain kind of silverware (*vaisselle godronnée*) ornamented in this manner. The appearance of the non-injected and that of the injected ligament are shown in Fig. 69. This supposed passage is usually called the *canal of Petit*.[3] The imperfect chambers in which the

[1] Syn.: *recessus cameræ posterioris;* spaces of Kuhnt, being described by him in his article "Ueber einige Altersveränderungen im menschlichen Auge," Ber. ü. d. Versamml. d. ophth. Gesellsch., Stuttgart, 1881, xiii. 38.

[2] Syn.: *ligamentum suspensoria lentis; zonula Zinnii;* zone of Zinn, for J. G. Zinn, who first described it in his "Descriptio anatomica oculi humani," Gottingæ, 1755; zonula; ciliary zone; *orbiculus capsulo-ciliaris; lamina ciliaris.*

[3] From François Pourfour de Petit, oculist at Paris, 1664–1741. See Mém. de l'acad. de Paris, 1723, p. 54.

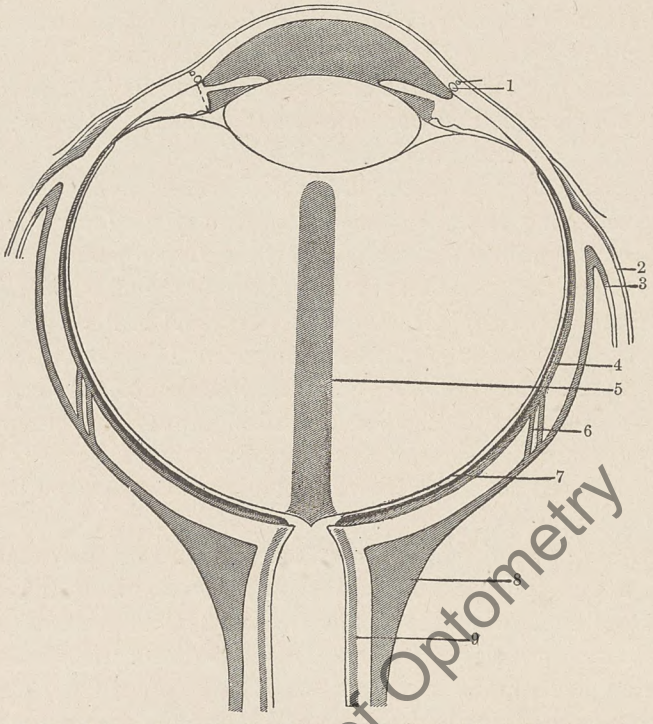
Syn.: *canalis Petiti; circulus Petiti; camera tertia aquosa;* post-zonular lymphatic space.

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air is engaged during the experiment are sometimes called the *zonular spaces*.[1] It is also possible to inject a viscous material like albumin between the anterior and the posterior fibres of the zonula, making an artificial passage known as the *canal of Hannover*.

Most anatomists consider that the hyaloid membrane blends completely in front with the capsule of the lens, which, in fact, represents it; but Stuart[2] describes it as continuous over the hyaloid fossa.

FIG. 70.



Lymphatic spaces of the eyeball. (Fuchs.)—1, sinus venosus; 2, 3, Tenon's capsule; 4, perichorioidal space; 5, hyaloid canal; 6, perivascular space about vorticose veins; 7, Tenon's space; 8, supravaginal space; 9, intervaginal space.

The *hyaloid canal* is a passage, some two millimetres in width, that directly traverses the substance of the vitreous, being the vestige of a perivascular space that in fœtal life surrounded the hyaloid artery. In front of the optic disk it enlarges to a space of about the same diameter as the disk, known as the *area Martegiani*.[3] A similar enlargement behind the lens is called the *post-lenticular space*.[4] (See Fig. 65.) These lymph-

[1] Syn.: *spatia zonularia*.

[2] Stuart (T. P. A.). On a Membrane limiting the Fossa Patellaris of the Corpus Vitreum. Proceedings of the Royal Soc., Lond., 1891, xlix.

[3] From Francesco Martegiani, who described it in his "Novæ observationes de oculo humano," Napoli, 1814, p. 19.

[4] Berger. Anatomie normale et pathologique de l'œil.

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passages communicate in front by means of the zonular spaces with the anterior chamber; behind they are continuous with the intervaginal spaces of the optic nerve. (See Fig. 70.) Coloring matter injected into the anterior chamber passes into the hyaloid canal (Michel), and from thence along the nerve (Schwalbe). Remains of the hyaloid artery may usually be found in the canal, even in the adult.

The *substance* of the vitreous, as distinguished from its capsule, is composed of a large amount of watery fluid, the *vitreous humor*,[1] and from one and a half to two per cent. of structural material, known as the *stroma* of the vitreous.[2]

It is a perfectly transparent material, having a refractive index about that of distilled water.[3] It is very liable to be affected by materials absorbed from the blood; for example, it may be colored orange by the administration of madder, and it may be tinged by the bile-pigments during an attack of jaundice. Its weight is from 6.7 to 8.3 grammes, and its specific gravity, according to Chenevix, is 1.005.

When freshly removed from the eye the vitreous substance has a somewhat sirupy consistency; but placed upon the meshes of a sieve its watery constituents drain away, leaving a slight residue that represents its structural elements.

FIG. 71.

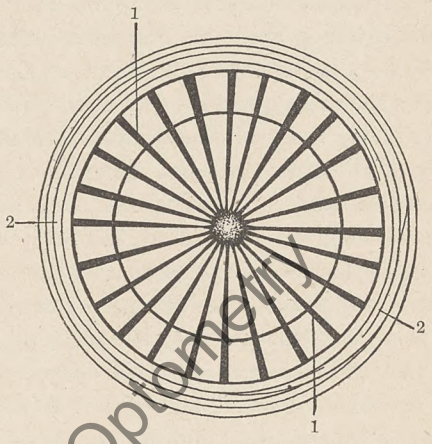


Diagram of supposed structure of the vitreous body as shown by an equatorial section. (Testut.)—1, 1, radial divisions; 2, 2, concentric divisions. The hyaloid canal is seen at the centre.

A long controversy has been waged with regard to the intimate structure of the vitreous. The entire substance appears to be separated into compartments by means of septa which at the periphery are concentric, or nearly so, while towards the centre they become radial. (See Fig. 71.) The number of radii is differently estimated by different observers, Schwalbe counting about thirty-seven, while Hannover reckons them at one hundred and eighty. It should be stated that the existence of a real structure in the vitreous is doubted by many competent observers.

Certain connective-tissue cells and leucocytes are found in small numbers within the vitreous. These may occasionally give rise to those entoptic phenomena known as *muscæ volitantes*, or floating specks. Crystals of

[1] Syn.: *humor vitreus; vitrina oculi.*

[2] Syn.: *stroma vitrei.*

[3] Krause gives its refractive index as 1.33485, that of water being 1.3342. Helmholtz fixes it at 1.33382, water being 1.33365.

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cholesterin are occasionally found floating in it, and present a peculiar glittering appearance under the ophthalmoscope.

A certain amount of the vitreous may be removed without seriously injuring vision, and it seems to be rapidly renewed. Operative interference with it is, however, usually to be avoided. It may be wounded during the extraction of cataract by cutting through the suspensory ligament, and may then drain away and cause an embarrassing complication.

In reaction the vitreous humor is alkaline. Half of its solids, which are but from 1.69 to 1.98 per cent. of the whole, are chloride of sodium and carbonate of sodium. Its composition seems, in fact, to differ from that of the aqueous humor mainly in a slight excess of albumin.

Numerous experiments have been made to determine the source of the secretion of the vitreous humor. Those of Deutschmann, which show its absorption after removal of the ciliary processes, have already been mentioned. Its greater richness in albumin may probably be accounted for by its less rapid renewal. Experiments made by injecting into the eyes of animals ferrocyanide of potassium or fluoresceine, although somewhat contradictory in their results, seem to show, on the whole, that fluid passes from the ciliary processes through the zonula into the vitreous chamber.[1]

Stilling[2] was of the opinion that the vitreous humor was removed by way of the optic disk and along the optic nerve. His views are not supported, however, by recent observers, and it seems probable that Leber is correct when he states that the only well-established channel for the exit of fluids from the eye is that at the angle of the anterior chamber, and that if any fluid leaves along the nerve it must be very slight in amount.

During fœtal life the vitreous body is well supplied with blood-vessels by the hyaloid artery, a branch of the central artery of the retina that runs in the hyaloid canal and gives off numerous branches to the substance. These all degenerate, and appear only as vestiges during adult life. As is

[1] Upon this subject see the following:

Ulrich (R.). Neue Untersuchungen über die Lymphströmung im Auge. Arch. f. Augenheilk., 1889, xx. 270.

Leplat (L.). Études sur la nutrition du corps vitré. Ann. d'oculistique, 1887, xcviii. 89.

Gifford. Weitere Versuche über die Lymphströme und Lymphwege des Auges. Arch. f. Augenheilk., 1893, xxvi. 308.

Nicati. La glande de l'humeur aqueuse. Archives d'ophtalmologie, 1890, 1891, x. 481, xi. 24, 152.

Pflüger. Zur Lymphcirkulation im Auge. Arch. f. Augenheilk., 1894, xxviii. 351.

Schick (H.). Experimentelle Beiträge zur Lehre von Flüssigkeitswechsel im Auge. Inaug. Diss. von Marburg, 1885.

Ehrenthal (W.). Kritisches und Experimentelles zur Lehre vom Flüssigkeitswechsel im Auge. Inaug. Diss. von Königsberg, 1887.

Panas. Études sur la nutrition de l'œil. Arch. d'ophtal., 1887, vii. 97.

Rampoldi. Sul passagio sperimentale della fluoresceina nella camera anteriore. Ann. di ottalm., 1887, xvi. 250.

[2] Stilling (J.). Ueber die Pathogenese des Glaucoms. Arch. f. Augenheilk., 1886, xvi. 296.

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well remarked by Rauber, the arteries supplying this region tend towards degeneration, in contrast with those of the retina, which tend towards greater development.

Since the adult vitreous possesses no proper vessels of its own, it depends upon those of the retina or of the chorioidal tract for its nutrition. Hence it is almost always involved in retinitis or chorioiditis.

THE INTRA-ORBITAL PORTION OF THE OPTIC NERVE.

When we compare the optic nerve[1] with the spinal nerves and most of the cranial ones, such striking differences are disclosed that it becomes evident that if the nomenclature were to be revised on a strictly morphological basis, we should not class the structure as a nerve. It is formed in the course of development as an outgrowth from the sides of the third ventricle, being the pedicle of the optic vesicle, and is, therefore, a commissural tract, like the peduncles of the cerebellum or the olfactory tract. This view is also sustained by its intimate structure, as it does not, like nerves, contain well-developed nerve-fibres ensheathed with a neurilemma, but those which have, like the white fibres of the brain and spinal cord, a sheath of myelin sustained by interfibrillary neuroglia. Neuroglia or "spider" cells are also found within its substance. This similarity to white fibre-tracts is also shown in pathological conditions. Atrophy of its fibres often occurs simultaneously with atrophy of other tracts within the brain and cord.

On entering the orbit, the optic nerve, which is closely united only to the upper side of the optic foramen, loses the flattened character which it had within the cranium and becomes approximately round. While passing through the foramen the ophthalmic artery lies to its outer side and below it. Immediately afterwards it traverses the fibrous funnel formed by the conjoined tendon[2] of the four recti muscles of the eye. In this situation it is accompanied by the artery and by those structures which have entered the funnel by passing through the lower part of the sphenoidal fissure. These are the ophthalmic vein, and the oculo-motor, abducens, and naso-ciliary nerves, the latter being a branch of the ophthalmic division of the trigeminus. The trochlear nerve and the other branches of the ophthalmic division pass through the upper part of the sphenoidal fissure, lie exterior to the muscles, and do not enter the funnel.

It receives several investments derived from the neural structures within the cranial cavity. The dura, continuous with the periosteum of the orbit, sends upon the nerve an external sheath that passes as far as the eyeball, blending there with the sclera. In a similar way the pia also envelops the nerve with a vascular sheet which serves for its nutrition, forming an inner sheath of the nerve. Between these there is left a lymphatic space, *the*

[1] Syn.: *nervus opticus;* second pair.

[2] Syn.: *annulus tendineus communis; annulus Zinnii;* tendon of Zinn. First mentioned by Zinn in his Descriptio oculi humani, Gottingæ, 1755.

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intervaginal space. An incomplete sheath of delicate trabecular tissue, derived from the arachnoid of the brain, lies between the dural and pial sheaths, dividing the intervaginal space into two,—an external, narrow, *subdural space,* and an internal, wider, *subarachnoid space.* These communicate through the optic foramen with the corresponding spaces of the cerebral meninges and contain cerebro-spinal fluid.

Within the orbit the nerve passes a little sideways and downward to reach the eyeball, describing a long sigmoid curve in the horizontal plane. In the vertical plane there is a somewhat abrupt downward sweep, followed by a straight course. These curves cannot, however, be said to be constant, as numerous individual varieties occur. They are apparently connected with the mobility of the eyeball, being more marked in animals that have very movable eyes,—such, for example, as the chameleon, that can direct each eye separately in any direction,—and only slightly developed in birds, who move their eyes but little, directing the vision rather by movements of the entire head. In exophthalmos, a disease characterized by an extrusion of the ball, the more marked the displacement the less mobile the eye becomes.

Weiss[1] has made a series of investigations concerning the frequency of these curves and their effect upon the condition of the eye. In sixty subjects he found the average length of the nerve from the optic foramen to its penetration of the sclera to be twenty-four millimetres, the greatest length found being thirty millimetres, the least twenty millimetres. The direct distance, measured from the foramen to the sclera, averaged, however, eighteen millimetres, there being a maximum of twenty-four millimetres and a minimum of fourteen millimetres. There is, therefore, in all eyes a surplus of length allowed to the optic nerve which admits a certain amount of play of the ball. This surplus, or *slack* of the nerve (Abrollungsstrecke of Weiss), averages five and six-tenths millimetres, having a maximum of twelve millimetres and a minimum of three millimetres.

The importance of this extra length in the optic nerve will be appreciated when the peculiarity of the eye-movements is considered. The ocular muscles are so inserted upon the ball that they turn it about a centre that coincides very nearly with the centre of figure. Consequently, in directing the vision towards any object, the posterior pole passes through the same arc as the anterior one, and if it is not freely movable the optic nerve will suffer more or less traction. In movements of extreme convergence the nerve becomes nearly straight, and may in some cases be stretched enough to affect the disk. Weiss found that when the amount of slack is above seven and a half millimetres, the nerve is never stretched, no matter how great the movements of the eye may be; when from seven and a half to five and a half millimetres, the nerve is dragged in excesssive movements and a transverse deformity of the disk sometimes occurs; in case the

[1] Weiss (Leopold). Beiträge zur Anatomie der Orbita, ii. Theil. Tübingen, 1890.

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slack is less than five and a half millimetres, the nerve is dragged, the disk deformed, and the alterations known as conus appear.

The orbital fat surrounds the nerve throughout its course. The ophthalmic artery, as it passes forward, ascends towards the roof of the orbit, and lies between the nerve and the superior rectus muscle. The central artery of the retina, accompanied by the central vein and an extremely delicate plexus derived from the ciliary nerves, penetrates the optic nerve about fifteen millimetres behind the ball. The vein usually lies behind the artery, while the plexus surrounds it.[1] They soon gain an axial position within the nerve, being there surrounded by a sheath of connective tissue. Deyl[2] has recently made a series of investigations to determine the correctness of the observations of Vossius with regard to the entrance of the vessels. His examinations were made with special care, the orbit being usually opened from below. He found that in each of twenty-one eyes examined by him the entrance was in the inferior nasal quadrant of the nerve. As this is the situation of the optic fissure of the embryo, it appears that the vessel maintains its primitive position, and that the supposition that the nerve and the eyeball have turned through an angle of ninety degrees during development is without foundation.

At its entrance into the orbit the nerve is surrounded by the four recti muscles. The *rectus superior* and *medialis* have, in fact, regular insertions upon its sheath, and it is probably because of this attachment that movements involving these two muscles are especially painful during inflammation of the optic-nerve sheath. As the nerve passes forward, the muscles diverge to their insertions upon the globe of the eye. The nerves of the orbit that have entered at the sphenoidal fissure likewise attend the optic nerve in its passage, the lower branch of the oculo-motor nerve, accompanied by the ciliary ganglion, lying nearest and along its lateral side. At its entrance into the globe the ciliary arteries and nerves surround the nerve.

Immediately before piercing the ball the nerve becomes contracted, for the reason that its fibres here lose their perineural sheaths.

The fibres of which the optic nerve is composed differ considerably in size, and this is probably connected with differences in function. They are arranged in parallel bundles separated from each other by septa derived from the pial sheath. The bundles in front of the entrance of the optic nerve are smaller than those behind it, and, as they here admit the cross-bands of the lamina cribrosa, they present the peculiar "rush-pith" appearance characteristic of the nerve.

It is important for us to understand the general grouping of the fibres, with reference both to their distribution upon the retina and to their intracranial connections. This arises from the fact that they must be con-

[1] Testut (Anatomie humaine, vol. ii.) speaks of this plexus as "Tiedemann's nerve."

[2] Deyl (J.). Ueber den Eintritt der Arteria centralis retinæ in den Sehnerv beim Menschen. Anatomischer Anzeiger, 20 März, 1896, xi. 687.

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sidered as avenues of conduction, and that a lesion of any portion is accompanied by disorders in corresponding areas of the retina or of the nerve-tracts within the cranium. A tumor or a piece of bone pressing upon the nerve may cause disturbances of vision that indicate accurately the situation of the lesion. As direct anatomical investigation gives no reliable information as to the course of particular fibre-bundles, it is necessary in such cases to have recourse to other methods. The discovery that the axis-cylinder processes of nerve-cells atrophy when the cells to which they belong are destroyed, assists us in this matter, as it is known that the nerve-cells whose axis-cylinder processes appear in the optic nerve are mainly situated in the retina. By observing the atrophied portions of the nerve in persons who have lost an eye when young, or by noting the appearances in the nerves of those who have lost vision in some restricted part of the retina, we can determine with some accuracy the general features of distribution.

First, we may ask the situation of the fibres that serve for most distinct vision. In the retina these are distributed to the fovea centralis and macula lutea, and a bundle of them that passes from the disk to the macula is known as the *papillo-macular bundle.* (Bunge.) In cases where vision is lost in this region (central scotoma), an atrophied bundle is found in the nerve, occupying a wedge-shaped area having its point at the central vessels and lying in the lower temporal sector. Behind the vessels it seeks a more central situation and has an oval form. At the chiasma it lies in the dorsal half of that structure. The area of this bundle is proportionately very large, amounting to one-third the area of the nerve.

It is well established that in man and other animals having the faculty of seeing objects with both eyes at once (binocular vision) the optic nerve contains fibres not only from the opposite side of the brain (crossed) but also from the same side (direct or uncrossed). An examination of animals in whom a single eye has been extirpated shows that the smaller, direct bundle lies at the temporal side of the disk and of the optic nerve, being surrounded, however, in the latter situation by crossed fibres which separate it from the sheath. In front of the entrance of the central vessels the crescent-shaped area of the direct fibres is divided into two portions separated by a transverse area of crossed fibres.[1]

Those fibres that are situated nearest the margin of the nerve and those found near the central vessels usually atrophy during old age.

[1] Schmidt-Rimpler. Archiv f. Augenheilkunde, xiv., Abth. iii.

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THE MICROSCOPICAL ANATOMY OF THE EYEBALL.

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THE bulbus oculi consists of three coats:

1. The *External Fibrous Tunic*, comprising the sclerotic and the cornea, upon which devolve the maintenance of the form of the organ and the protection of the more delicate structures enclosed.

2. The *Middle Vascular Tunic*, including the choroid, the ciliary body, and the iris, parts to which the principal vascular supply of the eye is distributed, with the exception of the vessels ramifying within the retina.

3. The *Inner Nervous Tunic*, the retina, which receives the terminal expansion of the optic nerve and contains the specialized neuroepithelium concerned in the perception of the visual stimulus. The aqueous humor, the crystalline lens, and the vitreous body are enclosed by these coats, and represent the refractive media of the eye.

An important division of the structures composing the visual organ is that based upon their embryonic origin, since the several parts of the eye may be grouped under two headings:

1. Those parts developed from the ectoderm.

2. Those parts developed from the mesoderm.

The members of the first group may be subdivided into:

a. Structures derived directly from the ectoderm, including the lens and its anterior epithelium, and the epithelium of the cornea and of the adjacent scleral surface.

b. Structures derived secondarily from the ectoderm through the optic vesicles protruded from the involuted ectoderm of the primary cerebral vesicles. To this group belong the primary retinal tissues, including the pigment-layer as well as the atrophic retinal layers continued over the posterior surface of the ciliary body and the iris.

All other parts of the eyeball, comprising the remaining portions of the sclera, the cornea, the iris, the ciliary body, the choroid, and the vitreous body, as well as the connective-tissue ingrowths of the retina, are developed from the mesoderm.

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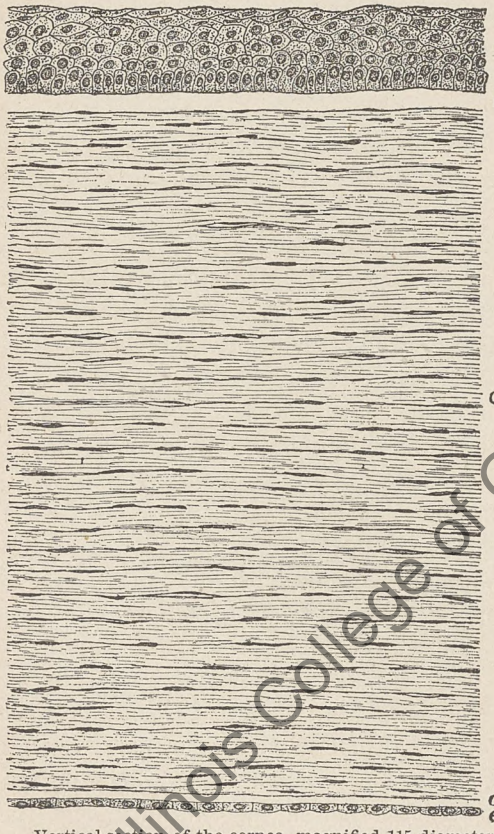
THE CORNEA.

The human cornea, which varies in thickness from .08 millimetre at the centre to 1.1 millimetres at the periphery, when viewed in vertical section in suitably prepared specimens exhibits five layers. (Fig. 1.) From without inward these are:

1. The anterior epithelium.
2. The anterior limiting membrane.
3. The corneal substance proper.
4. The posterior limiting membrane.
5. The posterior endothelium.

Referred to its development, the anterior epithelium alone is ectodermic in origin, the remaining layers being all the direct products of the mesoderm. At an early stage in the formation of the eye the lens is separated from the external ectodermic epithelium by a sheet of mesodermic tissue the inner surface of which is closely applied to the primitive lens and the outer to the ectoderm. This mesodermic tract differentiates into an outer thicker and more compact stratum and an inner much thinner and looser lamella; the inner layer becomes highly vascular, while the outer contains no blood-vessels. These strata are separated, after a time, by the formation of a distinct cleft, which represents the earliest appearance of the anterior chamber. The cleavage of the mesodermic tract thus effected defines the tissues of the primitive cornea from those of the vascular pupillary membrane. The corneal lamella is directly continuous with the scleral tissue; the pupillary, with the primitive choroidal tract. The innermost layers of the cornea—the posterior limiting membrane and the endothelium—bear, however, a par-

FIG. 1.



Vertical section of the cornea, magnified 115 diameters. —*a*, the anterior epithelium; *b*, the anterior limiting membrane; *c*, the corneal substance proper; *d*, the posterior limiting membrane; *e*, the posterior endothelium.

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ticularly close relation to the choroidal tract, the mesodermic layers of the cornea thus manifesting variation in their genetic affinities.

In view of these embryological data, Waldeyer[1] and, later, Schwalbe[2] have adopted a division of the cornea into three primary lamellæ:

1. *Pars conjunctivalis*, including the anterior epithelium.

2. *Pars scleralis*, including the substantia propria and the anterior limiting membrane.

3. *Pars choroidalis*, including the posterior limiting membrane and the endothelium.

The *anterior epithelium* covers the outer surface of the cornea, and is directly continuous with that covering the adjacent parts of the sclera and lining the conjunctival sac; it is, therefore, in continuity with the epidermis of the surrounding skin, a relation emphasized by the primary unbroken extension of the ectoderm over the corneal area before the appearance of the eyelids. This epithelial layer consequently is homologous with the epidermis, but differs from the latter structure in remaining permanently less highly developed, retaining the amphibian type (Minot),[3] as characterized by fewer cell-layers than usually compose the surface covering and by the absence of the stratum corneum.

The corneal epithelium belongs to the stratified squamous group, and consists of from six to eight layers of cells whose combined height constitutes an epithelial stratum which measures about .045 millimetre in thickness in the vicinity of the centre, and nearly double as much (.08 millimetre) at the periphery of the cornea.

In common with other epithelial lamellæ of the stratified squamous variety, the corneal epithelium is made up of cells presenting marked differences in the various layers. Three principal types of elements are seen: 1, the columnar cells of the deepest stratum; 2, the polyhedral cells of the middle layers; and, 3, the thin expanded plates of the superficial planes.

The cells of the deepest stratum constitute a single row of irregular columnar elements, which, while presenting considerable variation in their individual outlines, possess in common a more or less expanded basal surface, resting upon the subjacent anterior limiting membrane, and a rounded outer end received among the elements of the superimposed layer. The general form of these columnar cells (the "Fusszellen" of Rollett[4] and of Lott[5]) is somewhat club-shaped, their broad inner ends being often separated from the enlarged outer extremities by an intervening constriction, although the latter is sometimes so slightly marked that the typical cylindrical form

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[1] Waldeyer: Mikroscopische Anatomie der Cornea, Sklera, Lider und Conjunctiva, Handbuch der gesammten Augenheilkunde von Graefe und Saemisch, Bd. I., 1874.

[2] Schwalbe: Lehrbuch der Anatomie der Sinnesorgane, 1887.

[3] Minot: Human Embryology, 1892.

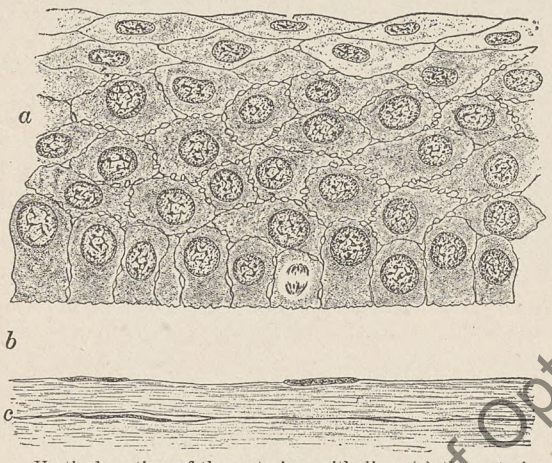
[4] Rollett: Ueber die Hornhaut, Stricker's Handbuch der Lehre von den Geweben, 1870.

[5] Lott: Ueber den feineren Bau und die physiologische Regeneration der Epithelien, insbesondere d. Cornealepithels, Centralblatt f. d. med. Wissensch., No. 37, 1871.

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is preserved. The presence of a distinct, highly refracting basal plate, as described by Rollett and Lott, is not to be demonstrated in accurately fixed and stained preparations, the expanded inner borders of the cells appearing as sharply defined smooth boundaries as figured by Waldeyer. Indications of the serrations pictured by Langerhans[1] are to be seen in tissue fixed in osmic acid, but it is probable that the methods of isolation formerly employed were responsible in no slight degree for the appearance of the toothed basal border. The columnar cells possess round or oval nuclei which occupy the outer ends of the cells. In the tissue of young animals particularly, but also occasionally in that of the adult, the presence of nuclei in various stages of division, as shown by the karyomitotic figures (Fig. 2), is not uncommon, since the formation of the new cells necessary for the replacement of the older surface-elements devolves upon the deepest layer of the epithelium, which possesses the greatest vital activity. The results of such cell-multiplication are seen as smaller irregular elements lying between the usual columnar cells.

FIG. 2.



Vertical section of the anterior epithelium (*a*), the anterior limiting membrane (*b*), and the superficial lamellæ of the substantia propria of the cornea: magnified 500 diameters.

The middle epithelial layers are made up of polyhedral cells whose details vary with their position. Those immediately succeeding the columnar elements are modified by the outer rounded ends of the latter, so that their deeper surfaces exhibit alternating depressions and ridges, which respectively receive the extremities of the lower cells and fill the interspaces between them.

The elements of the succeeding middle layers assume a more regular polyhedral form and possess conspicuous nuclei. Their outlines are not smooth, but broken by minute projections, which, as is common in similarly situated cells of the epidermis, bridge over the intercellular clefts and establish continuity between the protoplasm of the adjacent elements. When these are isolated the torn connecting threads produce the appearance of "prickle-cells."

The superficial layers of the corneal epithelium are composed of cells which have undergone gradual differentiation into the flattened, plate-like

[1] Langerhans: Ueber mehrschichtige Epithelien, Virchow's Archiv für patholog. Anatomie, Bd. LVIII., 1873.

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elements of the free surface closely resembling those covering many mucous surfaces. They differ from the elements composing the stratum corneum of the epidermis in possessing nuclei and in not being keratose. In passing towards the free surface the diameter of the cells increases as the thickness diminishes, so that the long axis of the surface plates is directed parallel with the anterior corneal border and at right angles to the longest diameter of the cells of the deepest stratum.

The elements of the anterior epithelium are united by a small amount of semi-fluid intercellular cement-substance which is traversed in the middle layers by the connecting threads uniting the adjacent cells. The intercellular clefts represent channels by which nutrient juices may reach the individual epithelial elements. Occasional migratory leucocytes are observed within these intra-epithelial spaces, as pointed out by Engelmann.[1] In the cornea of young animals, or in tissue subjected to irritative stimuli, cells exhibiting the nuclear manifestations of division are not uncommon.

The *anterior limiting membrane* (anterior basement membrane, lamina elastica anterior, anterior boundary layer, subepithelial stratum) is a specialized portion of the principal connective-tissue layer of the cornea, the outermost lamella of which appears as a distinct membrane in consequence of its unusual condensation.

This structure, which is very conspicuous in the human eye, varies greatly in its development and consequent prominence in different animals; while well developed in the rabbit, the guinea-pig, and many ruminants, it is less conspicuous in other mammals, as the pig, the cat, the horse, and the goat.

In the human cornea this membrane appears as a homogeneous, highly refracting band immediately beneath the anterior epithelium. The seemingly structureless layer measures from .018 to .020 millimetre in thickness in the centre of the cornea, and gradually decreases towards the periphery. Within one or two millimetres of the corneal limbus the anterior elastic membrane becomes greatly attenuated, and finally passes into the membrana propria beneath the conjunctival epithelium.

The true nature of this lamina as the differentiated outermost part of the substantia propria may be demonstrated by subjecting the corneal tissue to the action of potassium permanganate solution. By means of this reagent Rollett has shown that the seemingly structureless layer is resolvable into bundles of white fibrous tissue identical with those composing the bulk of the cornea. The assumed identity of the homogeneous tissue composing this layer with elastic tissue—emphasized by the misleading name "anterior elastic membrane" so often employed—is demonstrated to be erroneous by the solution of the anterior limiting membrane effected by prolonged boiling and the extended action of mineral acids. The usual cellular elements of the cornea are wanting within this stratum. The anterior limiting

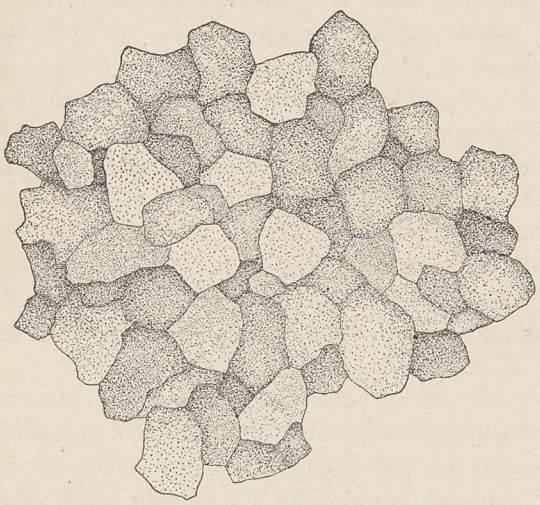
[1] Engelmann: Ueber die Hornhaut des Auges, 1867.

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membrane must probably be regarded as the homologue of the membrana propria supporting the epithelium of many mucous tracts. This relation is further emphasized by the presence of endothelioid plates, which may be demonstrated in certain animals, as the calf, lying upon the subepithelial surface of the substantia propria. (Fig. 3.)

The *corneal substance proper* (substantia propria, corneal stroma, ground-substance), notwithstanding its remarkable transparency and apparent homogeneity during life, possesses histological details of considerable complexity. The substantia propria consists of two principal parts:

FIG. 3.



Endothelioid markings on the anterior limiting membrane after treatment with silver: cornea of calf. Magnified 200 diameters. These markings do not correspond to those of the anterior epithelium, being much larger and less regular.

(*a*) A ground-substance, composed of bundles and lamellæ of fibrous tissue closely united by an interfibrillar cement-substance.

(*b*) Numerous connective-tissue cells, known as the corneal corpuscles, occupying interstices within the ground-substance.

The true character of the ground-substance is not suggested by its usual homogeneous appearance presented in ordinary preparations of the cornea, but is satisfactorily displayed only after the tissue has been subjected to the action of reagents capable of attacking the interfibrillar cement-substance which holds together and optically fuses the constituent fibres. One of the most important means of demonstrating the fibrous structure of the substantia propria is its treatment by a solution of potassium permanganate, successfully applied by Rollett in his classical investigations of this subject. Prolonged maceration in ten per cent. solution of sodium chloride (Schweigger-Seidel)[1] also effects dissociation of the fibrous tissue. Osmic acid, likewise, is of value in displaying the fibrous structure of the substantia propria, but for the demonstration of the form and disposition of the fibrous bundles no method yields more striking results than that of an interstitial injection of a one-fourth to one-half per cent. solution of silver nitrate into the substantia propria, with subsequent reduction of the silver by exposure to daylight. In such preparations (Fig. 4) the interfibrillar

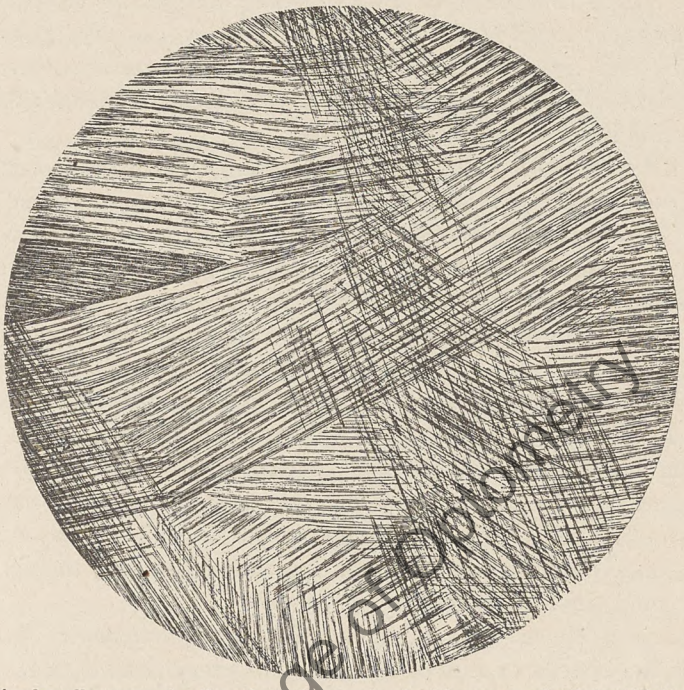
[1] Schweigger-Seidel: Ueber die Grundsubstanz und die Zellen der Hornhaut des Auges, Berichte d. sächs. Gesellsch. d. Wissensch., 1869.

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cement-substance becomes more or less darkly stained, while the fibrous tissue remains uncolored and contrasts as light lines against the darker surrounding ground.

The individual bundles of fibrous tissue cross one another at various angles, and are felted together into lamellæ from .008 to .010 millimetre in thickness; the bundles are disposed with considerable regularity with regard to the corneal free surface, sixty to sixty-five of such parallel strata usually being present in the human cornea. The separation of the cornea into distinct lamellæ, sometimes undertaken, must be regarded as artificial, since the number of the resulting isolated strata depends largely upon the skill with which the dissection is performed.

FIG. 4.



Interlacing lamellæ composing the substantia propria of calf's cornea, after interstitial injection of argentic nitrate solution and subsequent exposure to sunlight. Magnified 200 diameters.

The individual lamellæ are composed of the interlacing bundles of fibrous tissue, which in the human eye are irregularly disposed, in contrast to the definite arrangement of the bundles, almost at right angles, in the cornea in certain animals, as the frog. While the majority of the bundles extend in the general plane of the lamellæ, others pass obliquely, and serve to unite still more intimately the fibrous constituents of the stratum. Additional bundles pass beyond the limits of the individual layer and connect the adjacent surfaces of different lamellæ, thus materially contributing to the firmness of their union.

The anterior layers of the cornea, immediately beneath the limiting

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membrane, contain oblique or vertical bundles in unusual numbers; these delicate bands extend through the superficial strata towards the anterior limiting membrane, in the compact structure of which they fade away. Such curved bands constitute the *fibræ arcuatæ*, or supporting fibres; they are, however, only unusually oblique interlacing bundles of the fibrous tissue, and not independent structures.

In addition to the longitudinally and obliquely cut bundles constituting the corneal lamellæ, sections of tissue preserved in dilute spirit (forty-five per cent.) display punctations occupying the intervals between the bundles: these markings represent the transverse sections of the individual fibres composing the bundles extending approximately at right angles.

When corneal sections are examined by polarized light, the transversely cut bands remain constantly dark when viewed between the crossed Nicol's prisms; those cut longitudinally or obliquely, on the contrary, appear alternately dark and light (His).[1] Experiments with the entire cornea under polarized light indicate a preponderance of meridionally coursing fibres over those running in other directions (Rollett).[2]

The fibres composing the bundles and lamellæ of the ground-substance are intimately united by means of an interfibrillar albuminous cement-substance. The refractive indices of the latter and the fibrous tissue during life are identical, the cornea apparently being homogeneous and without structure.

The results obtained by boiling the substantia propria differ somewhat from those following like treatment of ordinary connective tissue, since the substance so secured resembles chondrin obtained from cartilage rather than gelatin yielded by connective tissue. Both gelatin and chondrin, however, as shown by Morochowetz,[3] consist of collagen and mucin, derived respectively from the fibrous elements and the cement-substance of the tissues. The peculiarity of the corneal tissue depends upon the relatively large proportion of interfibrillar cement-substance present, which yields a greater amount of mucin than is usually found in connective tissue, therein resembling the composition of chondrin.

The Corneal Spaces.—Examination of vertical sections of the cornea shows that the lamellæ of fibrous tissue are not everywhere in close contact, but are separated in many places by intervening clefts; the latter constitute the *corneal spaces*. Seen in section, these appear as narrow fusiform cavities the tapering ends of which fade away between the opposed laminæ, or, at best, are traceable as minute crevices between the fibrous bundles, sometimes as far as the neighboring dilated spaces into which they open.

A satisfactory display of the arrangement of the corneal spaces, however, is had only after the treatment of the tissue by silver staining; by means of this reagent the generously distributed cement-substance is colored

[1] His: Beiträge zur normalen und pathologischen Histologie der Cornea.

[2] Rollett: loc. cit.

[3] Morochowetz: quoted by Halliburton, Chemical Physiology and Pathology, 1891, p. 484.

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brown, while the spaces, remaining almost unaffected, appear as light figures on the dark background. Seen in successful silver preparations, the corneal spaces appear as light irregularly stellate areas, as shown in Fig. 5, from which minute ramifications, the *corneal canals*, extend in various directions and establish communication with the adjacent corneal spaces.

Fig. 5.



Surface view of silvered cornea, showing the intercommunicating corneal spaces (*s*) lying within the deeply stained ground-substance (*g*). Magnified 480 diameters.

These spaces and their extensions, while constituting a system of intercommunicating channels throughout the substantia propria, are not peculiar to the cornea, but represent the system of lymph-spaces present in other dense connective tissues, conspicuous examples of which are seen in the central tendon of the diaphragm, and particularly in bone. Just as the lacunæ and the canaliculi of the latter tissue form lymph-tracts through osseous structures, so the spaces and canals of the cornea afford channels for the conveyance of nutritive tissue-fluids throughout the non-vascular substantia propria. These spaces or "juice-channels," then, must be regarded as parts of the interstitial lymphatics of connective tissue.

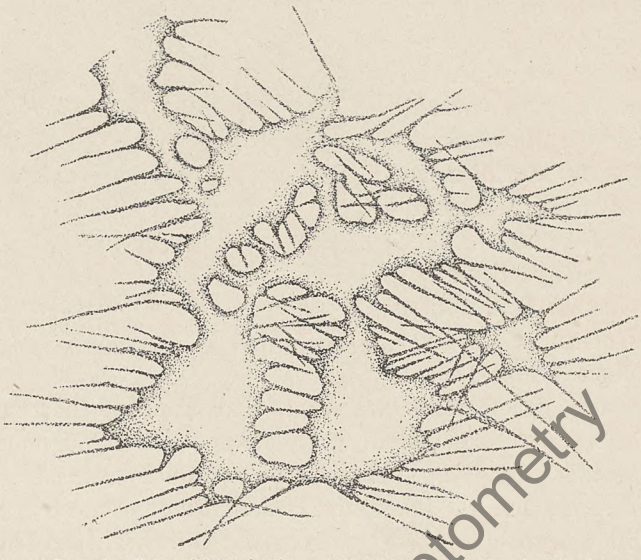
In addition to the "negative" pictures of the corneal spaces obtained by the now classic silver method of v. Recklinghausen, according to which the fresh tissue is immersed in .5 to 1 per cent. solution of argentic nitrate and subsequently exposed to sunlight until the silver albuminate formed by the cement-substance has been darkened, silver staining may be employed to yield "positive" views of the spaces, as shown in the accompanying Fig. 6. Positive pictures of the corneal lacunæ and canaliculi of great beauty may often be secured by an interstitial injection of the fresh cornea with .2 to .25 per cent. solution of silver nitrate and subsequent reduction in sunlight. When successful, the silver deposit outlines with remarkable clearness the spaces, and fills more or less completely the delicate radiating canals. The exhibition of the spaces thus obtained probably differs from that by the usual silver impregnation in depending upon the reduction effected by the albuminous contents of the spaces rather than upon that induced by the surrounding cement-substance.

Other methods of demonstrating the existence of the corneal juice-channels include the interstitial injection of mercury (Bowman); of oily mixtures, especially turpentine and olive oils colored with alkanet root

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(Rollett); of olive oil followed by osmic acid (Schwalbe); of a solution of asphalt in chloroform (Retzius); and the impregnation of the tissues with solutions of potassium ferrocyanide and their subsequent reduction by means of ferric salts, as suggested by v. Wittich and v. Recklinghausen. The ingenious experiment of Genersich[1] proved the existence of the intercommunicating channels by the invasion of leucocytes secured by exposing the corneal tissue within the dorsal lymph-sac of living frogs; subsequent examination showed the presence of the migratory cells in large numbers within the spaces and the canals of the corneal tissue. The impregnation

FIG. 6.



Corneal spaces of ox after interstitial injection of argentic nitrate; "positive" picture. Magnified 450 diameters.

methods are to be preferred to injections, as yielding trustworthy pictures of the form and arrangement of the lacunæ and canaliculi, since, with the exception of slight shrinkage, the appearance of these spaces in preparations so made may be accepted as representing the actual relations within the living tissue: such pictures are in marked contrast to the abnormally distended and exaggerated condition of the spaces usually encountered after artificial injections. The presence of rows of closely placed minute lanceolate or irregularly oval figures, the so-called "corneal tubes," must be regarded as an artificial detail resulting from the interstitial injections employed for their demonstration.

The corneal spaces are found throughout all parts of the substantia propria, although some variation exists as to size and number. The super-

[1] Genersich: Zur Lehre von den Saftkanälchen in der Cornea, Wiener medicin. Jahrbücher, 1871.

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ficial lamellæ, immediately beneath the anterior limiting membrane, contain the smallest but most closely placed spaces; the deep lamellæ adjoining the posterior limiting membrane, on the contrary, have the largest but most widely separated lacunæ. The corneal spaces and canals do not possess distinct walls of their own, but are defined by the surrounding fibrous tissue and cement-substance, the latter particularly bearing a close relation to the clefts. (Fig. 7.)

Corneal Cells.—In addition to the tissue-juices contained within the system of spaces throughout the substantia propria as part of the usual contents of the lymph-radicles, the corneal spaces are occupied by conspicuous morphological elements, the *corneal corpuscles*, together with a variable, and usually very limited, number of migratory leucocytes, the *wandering cells*.

Fig. 7.



Surface view of silver preparation of corneal stroma of ox, showing relation of spaces to fibrous tissue. Magnified 450 diameters.

The corneal corpuscles are connective-tissue cells lodged within the minute lymphatic lacunæ of the substantia propria. The arrangement here found is by no means peculiar to the cornea, but corresponds with that seen in many other localities, repeating the general relation existing in other organs between the cells and ground-substance of dense connective tissues.

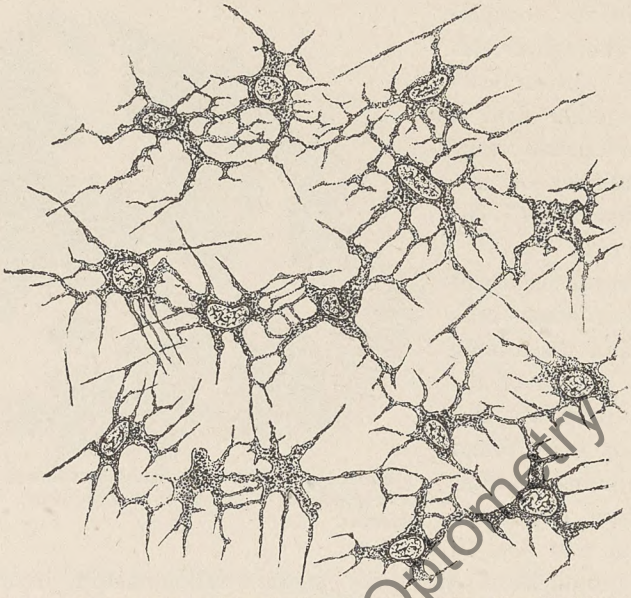
The presence of these elements may be appreciated in well-stained sections of the cornea, the cells appearing in profile as thin fusiform protoplasmic masses which usually adhere to some portion of the lenticular cavity into which they project and which they partially occlude. The completeness with which the cells fill the spaces in which they lie depends much upon the condition of the protoplasm, since when the latter has suffered shrinkage in consequence of the action of reagents the disproportion between the extent of the space and the size of the corneal corpuscle is exaggerated. The most careful fixation of the tissue points to the fact that during life the corneal cell almost completely occupies one of the broader walls of the space, with the outlines of which it often closely corresponds; the cell-body, however, does not equal in thickness the width of the lacuna, so that often a considerable cleft remains for the passage of the tissue-juices.

In many places, particularly in the course of the canaliculi connecting

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the adjacent lacunæ, the protoplasmic net-work formed by the union of the processes of the corneal cells by no means accurately corresponds to the outlines of the boundaries of the lymph-channels. Not infrequently two or more of the interlacing protoplasmic processes lie within a single canal, thus forming a net-work of much greater richness and complexity than that formed by the canaliculi and spaces. This discrepancy may be demonstrated in human corneæ, as suggested by v. Recklinghausen,[1] without reagents, by simply guarding against too rapid loss of the watery constituents, the cells and the spaces then appearing with great clearness.

FIG. 8.



Corneal corpuscles as seen in surface view in gold preparations. Magnified 480 diameters.

While the relation between the extent of the corneal spaces and the bulk of the enclosed cells is best appreciated, probably, in vertical sections, an adequate picture of the corneal corpuscles, as to their form and connections, is furnished by surface views alone.

Such preparations may be secured by several methods of staining, including those by carmine and hæmatoxylin, but for the exhibition of the corneal corpuscles impregnation with .5 per cent. solution of gold chloride and subsequent reduction have long been acknowledged as the classic method and one capable of yielding admirable although uncertain results. Silver staining, while ordinarily producing negative pictures, may be modified in its application so as to furnish admirable preparations of the corneal cells. Strong applications of lunar caustic to the living tissue and subse-

[1] Recklinghausen: Ueber die Saftkanälchen der Hornhaut, Anatom. Anzeiger, Bd. III., 1888.

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quent exposure to light, as shown by Stricker,[1] often result in beautiful demonstrations of the corpuscles stained, a peculiar purplish-brown tint of the protoplasm being indicative of the action of the silver upon the living cells.

When the perfectly fresh transparent cornea is examined, no trace of the elaborate net-work of protoplasmic processes of the corneal corpuscles is visible, and not until the tissue begins to lose its homogeneity of refraction are its histological details suggested. The cells subsequently become apparent as slightly opaque, delicately granular bodies within the still transparent ground-substance. The vapor of iodine applied to the corneal tissue while under observation brings to view the presence of the corpuscles in a very striking manner, the cells seemingly gradually growing into existence beneath the eye in a way to recall the formation of crystals. Iodine preparations of these elements, however, possess the disadvantage of not being permanent, since, notwithstanding their crisply defined pictures at the time, a few hours suffice for their complete disappearance.

Successful preparations of the cornea by either of the approved methods of staining display the same general picture of the corpuscles and their processes. Viewed from the surface, these cells appear as irregularly stellate, flattened bodies within the protoplasmic masses of which lie conspicuous oval nuclei. Numerous processes extend in various directions, often in different planes, from the body of the cell, and join, either directly or by means of secondary branches, similar prolongations from the neighboring corpuscles. The union thus effected establishes a more or less continuous protoplasmic net-work throughout the various corneal lamellæ, the cells lying within the same stratum being most closely associated.

The nuclei of the corneal corpuscles are very distinct, being limited by a nuclear membrane and traversed by numerous branching threads of deeply staining chromatin, which contrast sharply with the faintly colored intervening nuclear matrix. A nucleolus, and not infrequently two or even three pseudo-nucleoli, are usually to be distinguished, although in gold preparations the presence of these bodies is not always capable of satisfactory demonstration.

The relations between the corneal corpuscles and the spaces are interesting, since the disposition and limits of the system of intercommunicating juice-channels in a general way determine the arrangement of the protoplasmic cells and processes which they contain. In corneæ in which the component bundles of the substantia propria are grouped with great regularity, as in the frog, the intervening lymph-clefts are disposed with much greater regularity than in those cases, as in the higher mammals, where the interlacing of the corneal lamellæ is more intimate and less definite. This difference is very manifest on comparing gold pictures of amphibian and mammalian corneæ, in the first of which the cell processes extend as long,

[1] Stricker: Studien aus dem Institut f. experimentelle Pathologie in Wien.

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straight, protoplasmic threads running parallel with one another or crossing those of different planes almost at right angles. The cells of the mammalian corneæ, on the contrary, send processes in various directions and planes as branching and tortuous outrunners, the protoplasmic figures following the more complicated course of the lymph-channels between the irregularly disposed corneal bundles.

The corneal corpuscles are applied to one wall of the spaces, and their protoplasmic processes extend into the canaliculi, thus repeating, more or less accurately, the outlines of the system of lymphatic channels; the cells and their processes, however, probably never completely fill the lymph-canals, but are separated from the unoccupied wall by clefts, thereby affording a path for the tissue-juices. As already pointed out, the protoplasmic net-work is usually of greater delicacy and complexity than the lymph-channels, owing to the fact that not infrequently two or more processes lie within a single canal. In the corneæ of young mammals, as the kitten or the puppy, the larger spaces often contain several corpuscles which form a continuous more or less perfect lining applied to the walls of the cavities. Silver preparations of such tissue display the outlines of these cell-groups by markings closely resembling limited endothelial areas, which, in principle at least, these flattened adjoining connective-tissue cells really represent. The surfaces of contact between these elements are indicated by lines of deeply stained cement-substance just as in silver pictures of ordinary endothelium, the nuclei being brought to view by additional coloring with hæmatoxylin or carmine.

The Wandering Cells.—In addition to the corneal corpuscles proper, or the "fixed" corneal cells, careful examination sometimes reveals the presence of minute irregular or ovoid masses of granular protaplasm within the crevices between the corneal corpuscles and the walls of the spaces or the narrower lymph-canals; these bodies are the so-called *wandering cells* of the cornea.

Critical inspection of these elements shows them to be migratory leucocytes which have extended their journeys within the lymph-channels of the cornea, just as they invade the lymphatic spaces of other connective tissues. They are, therefore, not peculiar to the cornea, but are the representatives of widely distributed elements. The presence of leucocytes within the normal corneal tissue has been questioned, their advent being regarded as evidence of pathological change. There seems, however, to be ample reason for considering these migratory cells as transient guests of perfectly normal structures. The appellation "fixed" cells applied to the corneal corpuscles proper, as distinguished from the migratory elements, is not entirely accurate, since these bodies, in common with many other active connective-tissue cells, may display changes of form in response to the irritation of electricity, inflammation, or other stimuli. The notable increase in the number of the wandering cells witnessed during inflammatory processes affecting the cornea is probably due not only to congregation of the migratory leucocytes in

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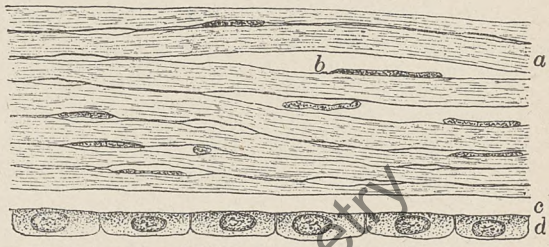
response to the unusual stimulus, but also to the production of new cells from the division of some of the fixed corneal corpuscles, as long ago convincingly demonstrated by Stricker and Norris.[1]

The form of the interfibrillar cleft in which the migratory cells lie has much to do with the contour of the individual elements; since, it is evident, the same protoplasmic mass may become greatly elongated or assume a more spherical outline according to the limits of the lymph-channel in which it is confined.

The Posterior Limiting Membrane (the membrane of Descemet, the posterior elastic lamina, the membrane of Demours, the inner basement membrane) constitutes an apparently homogeneous elastic lamella which separates the inner border of the substantia propria from the endothelium covering the posterior surface of the cornea. This layer differs from the anterior limiting membrane in its physical, chemical, and morphological characteristics.

It is much less intimately attached to the substantia propria than is the anterior membrane, as explained by the developmental relations of the corneal layers. Prolonged maceration in ten per cent. solution of sodium chloride effects its complete isolation from the fibrous tissue of the cornea. The separated membrane displays a marked tendency to roll together, with the anterior surface innermost, and resembles closely elastic tissue in its general appearance and behavior. Its marked resistance to the action of acids, alkalines, boiling water, and other reagents further distinguishes it from the anterior limiting membrane, while its identity with elastic tissue is called in question by its more rapid digestion in solutions of trypsin (Sasse).[2]

FIG. 9.



Vertical section of the posterior lamellæ of the cornea (*a*), together with the posterior limiting membrane (*c*) and endothelium (*d*); *b*, corneal cell in profile within a space. Magnified 500 diameters.

The posterior limiting membrane contains no cells, and, ordinarily, presents no indications of being composed of secondary lamellæ; after prolonged boiling in water, however, it is sometimes possible to resolve the membrane into a number of delicate structureless strata. Exceptionally, sections of silvered cornea under high amplification show traces of these component lamellæ. The membrane also differs from the anterior limiting layer in being thinnest at the centre and thickest at the periphery of the cornea, its thickness at these points being respectively .006 to .008 milli-

[1] Stricker und Norris: Versuche über Hornhautentzündung, Studien aus dem Institut f. exper. Pathologie in Wien, I., 1870.

[2] Sasse: Zur Chemie der Descemet'schen Membran, Untersuch. d. physiolog. Institut d. Univ. Heidelberg, II., 1879.

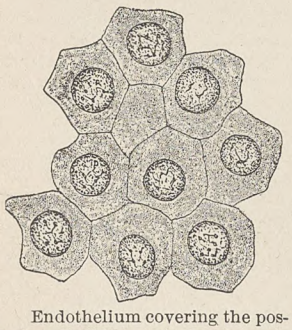
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metre and .010 to .012 millimetre. After middle life the membrane becomes somewhat thicker, in some instances measuring .020 millimetre; at the same time, not infrequently low papilliform elevations appear on the inner surface of the membrane and increase with age both in size and in number. At the periphery the posterior limiting membrane breaks up into numerous bands, which are continued from the sclero-corneal junction and become the structures occupying the anterior angle of the ciliary region; in this situation they are known as the *ligamentum pectinatum iridis*, of which a fuller description is given in connection with the spaces of Fontana.

The Posterior Endothelium, the endothelium of Descemet's membrane, covers the inner surface of the cornea and forms part of the lining of the anterior chamber of the eye. In view of its direct derivation from mesodermic tissue, this layer is properly regarded as endothelium, and not as epithelium.

The posterior covering of the cornea is composed of a single layer of thin polyhedral plates, the outlines of which, as displayed by silver-staining, present a mosaic of considerable regularity when the normal curvature and tension of the tissue are maintained. The individual cells possess the usual characteristics of endothelial plates, having an oval, sometimes reniform, nucleus situated somewhat eccentrically within the faintly granular cell-protoplasm. The nuclei are sometimes thicker than the remaining portions of the plates and project beyond the general level of the cell-surface; in such cases the line of the inner border of the endothelial layer, as seen in vertical sections, is not straight, but sinuous, the position of the nuclei then being indicated by slight elevations.

FIG. 10.



Endothelium covering the posterior limiting membrane seen from the surface. Magnified 500 diameters.

These cells, being subject to variations in tension due to relaxation of the cornea in the course of preparation, not infrequently present unusual pictures. Among such are cells with sinuous outlines or stellate forms, the projecting rays of the adjacent elements alone being in normal contact. The production of such star-like figures has been regarded by Schwalbe as depending upon the appearance of vacuoles within the intercellular cement; by others, as Klebs, and Stricker and Norris, the endothelial cells are regarded as possessing, especially under the influence of irritation, the power of contracting and of changing shape.

The remarkable details of the cells of Descemet's membrane described and pictured by Smirnow,[1] and later by Nuel and Cornil,[2] in the cornea of

[1] Smirnow: Ueber die Zellen der Descemet'schen Haut bei Vögeln, Internat. Monatsbl. f. Anat. u. Phys., Bd. VII., 1890.

[2] Nuel et Cornil: De l'endothélium de la chambre antérieure de l'œil, particulièrement de celui de la cornée, Archives de Biologie, t. x., 1890.

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the pigeon, duck, chicken, etc., include the presence of radiating bundles of fibrillæ which pass from near the nucleus of the endothelial cell across the intercellular space to the vicinity of the nuclei of the adjacent plates. The number of bundles of fibrillæ in general corresponds with the number of sides of the polyhedral elements, the bundles radiating and often overlapping those from neighboring cells. The fibrillæ rapidly disappear after death, accurate fixation of the living tissue being indispensable for their satisfactory demonstration. These interesting details appear to be limited to the cells of the corneæ of birds, since they are not found in the corresponding mammalian structures.

In common with those of other serous surfaces, the endothelial plates lining the anterior chamber are continually undergoing destruction, the effete cells being replaced by new elements, as indicated by the karyokinetic figures observed within the endothelium in suitably fixed tissue. The presence of minute openings between the endothelial cells along their lines of juncture, particularly at their angles, is demonstrated by silver stainings. These apertures or *stomata* are regarded by Ciaccio[1] as directly communicating with the system of lymph-channels situated within the ground-substance between the endothelium and the posterior elastic membrane.

The Blood-Vessels of the Cornea.—The normal cornea is non-vascular, except within a very limited zone at the extreme periphery. At the corneal margin the anterior limiting membrane fades away in a delicate layer of loose connective tissue lodged between the epithelium and the substantia propria. This narrow marginal zone contains the terminal vascular loops which encircle the cornea and alone represent its supply of blood-vessels. The vascular area, although very narrow, is not quite uniformly developed, being broadest above and below, where it measures 1–1.5 millimetres (at most 2.0 millimetres), and narrowest on each side, where it attains a width of .5–1.0 millimetre. The capillary loops composing this peripheral net-work are derived from delicate arterial stems continued from the anterior ciliary arteries through the episcleral branches. After passing the limbus the arterioles rapidly break up by dichotomous division into twigs of great delicacy, .005–.006 millimetre in width, which communicate with one another by numerous anastomoses and terminate in capillary loops forming a series encircling the cornea. The capillaries give origin to the wider venous radicles, the diameter of which, as determined by Leber,[2] is about double that of the arteries. The veins join the episcleral net-work and become tributaries to the anterior ciliary trunks. During fœtal life the peripheral parts of the cornea are invaded by the precorneal vascular net-work. This normally diminishes before birth to the limits already described, and probably at no time extends completely over the cornea, the

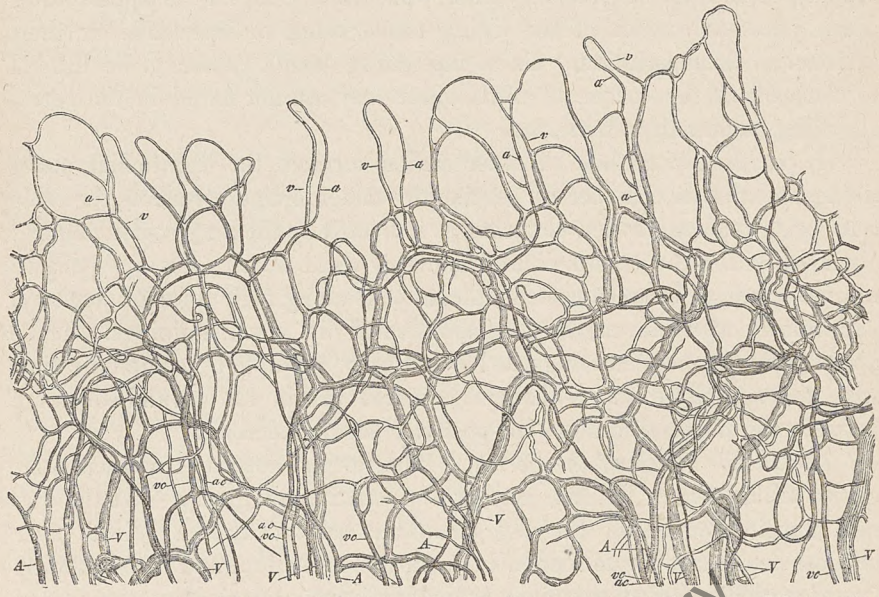
[1] Ciaccio: Osservazioni intorno alla membrana del Descemet e al suo endothelio, Memorie dell' accad. di Bologna, ser. III. t. v., 1875.

[2] Leber: Die Circulations- und Ernährungsverhältnisse des Auges, Graefe und Saemisch's Handbuch, Bd. II., p. 334.

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central portion remaining uninvaded. The more deeply situated vascular loops occasionally observed in the human cornea are probably to be referred to pathological processes, although in some animals, as the ox and the sheep, according to Richiardi,[1] such vessels normally exist.

FIG. 11.



Vascular net-work at the corneal limbus. (After Leber.)—*A*, *A*, episcleral branches of the anterior ciliary arteries; *V*, *V*, anterior ciliary veins, united by means of the episcleral venous plexus; *a*, *a*, *v*, *v*, the arterial and venous limbs of the marginal loops; *ac*, *vc*, anterior conjunctival arteries and veins given off from the episcleral vessels. Low magnification.

The Lymphatics of the Cornea.—The elaborate system of intercommunicating corneal spaces, as already pointed out, must be regarded as representing the lymph-tracts of the dense connective tissue of which the cornea is composed. In addition to these interstitial clefts, the larger nerve-trunks on entering the cornea are accompanied for a short distance—about one millimetre—by distinct perineural sheaths which are to be considered as lymph-channels into which the adjacent corneal spaces often directly open. These perineural canals number between sixty and eighty, and are lined with a more or less perfect covering of flattened endothelial plates.

The fluids occupying the corneal spaces are probably derived from two sources,—from the marginal vascular loops and from the diffusion from the anterior chamber. (Schwalbe.) The nutritive juices obtained from the peripheral vessels seem to be devoted particularly to the anterior epithelium and the more superficial layers of the substantia propria, while the fluids derived from the anterior chamber are especially destined for the nourishment of the deeper portions of the cornea.

[1] Richiardi: Sui vasi sanguiferi della cornea, Zoologisch. Anzeiger, No. 76, 1881.

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The presence of the posterior endothelium offers an insurmountable barrier to the loss of the aqueous humor by filtration into the cornea, since as long as the endothelial elements are intact, as pointed out by Leber, the escape of the aqueous humor is extremely insignificant. When, on the contrary, the cells covering the membrane of Descemet are removed, as after death, the corneal tissue rapidly becomes filled with the watery fluids, and, consequently, opaque. The possibility, however, of diffusion taking place, at least to a very limited extent, through the posterior layers of the

FIG. 12.



Perineural lymph-sheath lined by an imperfect endothelial layer; in two places corneal spaces directly communicate with the lymph-channels. Magnified 200 diameters.

cornea seems to be demonstrated by the experiments of Leber and Krükow[1] and of Knies,[2] in which, after injection of potassium ferrocyanide and subsequent treatment with iron chloride solution, not only the membrane of Descemet and the adjacent lamellæ of the substantia propria were found tinged, but also the intercellular cement-substance of the endothelium appeared as blue lines.

While limited diffusion may directly affect the lamellæ contiguous with the membrane of Descemet, the more usual path is by the circuitous route through the spaces of Fontana at the angle of the anterior chamber, and thence into the lymph-channels of the sclera which directly communicate

[1] Quoted by Schwalbe: Anatomie der Sinnesorgane, p. 164.

[2] Knies: Ueber die vorderen Abflusswege des Auges und die künstliche Erzeugung von Glaukom, Archiv f. Augenheilkunde, Bd. XXVIII., 1894.

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with those of the cornea. The importance of the indirect lateral path from the anterior chamber into the corneal tissue has been strongly emphasized by the recent investigations of Staderini,[1] which conclusively demonstrate the conspicuous rôle played by the spaces of Fontana and the scleral tissue in the escape of the contents of the anterior chamber.

Fluids conveyed within the lymph-channels pass into the surrounding corneal stroma through the especial agency of the interfibrillar ground-substance; the absorption thus effected results in the complete transference of the contents of the lymph-canals to the substantia propria, as demonstrated in cases where the corneal spaces are originally filled with colored fluids, the spaces after a time appearing empty and the ground-substance deeply tinged. The views of Straub,[2] that the contents of the lymph-channels are not uniformly distributed, but are directed under usual conditions particularly to those parts of the intercommunicating interfascicular clefts in which the corneal corpuscles are lodged, are at variance with the testimony of other observers, and are directly opposed by the later investigations of v. Recklinghausen[3] and of Gutmann,[4] which sustain the accepted doctrine of the preformation of definite paths for the uniform diffusion of the tissue-juices throughout the corneal stroma. Gutmann further succeeded in demonstrating a communication between the intercellular clefts within the anterior epithelium and the corneal spaces by means of injections of a solution of asphalt in chloroform, an observation of interest in view of the previous statements of Pflüger[5] maintaining the absorption through the anterior surface of the cornea.

Although diffusion may take place to a limited extent through the posterior surface of the cornea, as already pointed out, filtration of the aqueous humor into the corneal strata during life is prevented, probably to an absolute degree, by the presence of the endothelium of the membrane of Descemet. The impermeability of this layer is maintained even when subjected to unusual pressure, the fluid contents of the anterior chamber escaping by means of the passage-ways existing at the sclero-iridial angle.

The fluids collected within the system of corneal spaces are carried off by two principal outlets: (1) by the lymphatics of the conjunctiva; (2) by the perineural lymph-tracts. The first of these—the conjunctival lymph-tracts—constitute the most important channels for the escape of the contents of the intra-corneal lymph-paths; the spaces surrounding the nerve-trunks

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[1] Staderini: Ueber die Abflusswege des Humor Aqueus, Archiv f. Ophthalmologie, Bd. XXXVII., Abth. 3, 1891.

[2] Straub: Die Lymphbahnen der Hornhaut, Archiv f. Anat. u. Phys., Anat. Abth., 1887.

[3] v. Recklinghausen: Ueber die Saftkanälchen der Hornhaut, Anatom. Anzeiger, Bd. III., No. 19, 1888.

[4] Gutmann: Ueber die Lymphbahnen der Cornea, Archiv f. mik. Anat., Bd. XXXII., 1888.

[5] Pflüger: Zur Ernährung der Cornea, Klin. Monatsblatt f. Augenheilkunde, Bd. XX., 1882.

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FIG. 13.



Lymph-spaces of the pig's cornea, injected with asphalt-chloroform, showing communication between the corneal spaces (*a*) and the intra-epithelial clefts (*b*). (Gutmann.)

FIG. 20.



Lymph-spaces of the sclerotic of pig injected with asphalt-chloroform. (Gutmann.)

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also afford no insignificant exit, and serve to convey the lymphatic fluid within the perineural sheaths along the course of the anterior ciliary nerves. While the lymph-channels of the cornea and the sclera directly communicate, as well demonstrated by the investigations of Gutmann,[1] the distinctly smaller size of the spaces within the scleral tissue renders it improbable that the corneal juices pass into the sclera to any extent; on the other hand, direct observations show that the cornea receives no inconsiderable part of its tissue-juices by means of the sclerotic spaces.

The Nerves of the Cornea.—The nerves of the cornea, together with those of the ciliary muscle and the iris, are derived from the *ciliary plexus* formed by the long and short ciliary nerves. Those destined for the supply of the cornea proceed through the sclera, on the outer side of Schlemm's canal, to the vicinity of the corneal margin, where they unite to form an encircling net-work, the *plexus annularis.*

Two sets of fibres are given off from this plexus: 1. Twigs which, after obliquely piercing the sclera, pass to the conjunctiva and there join the conjunctival nerves in the formation of net-works supplying that structure; from the conjunctival plexus thus constituted a number of nerve-trunks are given off at the limbus, which enter the cornea and are especially destined for the supply of the anterior layers of that structure. 2. Additional and far more numerous corneal branches which are given off from the annular plexus and proceed directly, more or less radially arranged, to the substantia propria corneæ, which they enter well towards the membrane of Descemet.

The entire number of nerve-trunks thus entering at the corneal margin aggregates between sixty and eighty. The nerve-bundles are accompanied, as already mentioned, by enveloping perineural lymph-sheaths, for a short distance—about .75 to 1 millimetre—along their course within the corneal stroma. These trunks, which vary greatly in thickness,—some containing two or three nerve-fibres, others ten to twelve,—soon lose their medullary substance, becoming non-medullated within .5 to 1.5 millimetres after entering the cornea; they soon break up within the substantia propria into delicate fibrillæ, which take part in the formation of numerous plexuses.

Our knowledge concerning the arrangement and the ultimate distribution of the nerves within the cornea, derived from the investigations of Ciaccio,[2] Kölliker,[3] Hoyer,[4] Königstein,[5] Klein,[6] Waldeyer,[7] Ranvier,[8] and

[1] Gutmann: loc. cit.

[2] Ciaccio: On the Nerves of the Cornea, etc., Quart. Journal of Mic. Science, 1863.

[3] Kölliker: Ueber die Nervenendigungen in der Hornhaut, Würzburg. naturwis. Zeitschr, Bd. VI., 1866.

[4] Hoyer: Ueber die Nerven der Hornhaut, Archiv f. mik. Anatomie, Bd. IX., 1873.

[5] Königstein: Beobachtungen ueber die Nerven der Cornea u. s. w., Wiener Sitzungsber., 1877.

[6] Klein: The Termination of the Nerves in the Mammalian Cornea, Quart. Journal of Mic. Science, 1880.

[7] Waldeyer: Ueber die Endungsweise der sensiblen Nerven, Archiv f. mik. Anat., Bd. XVII., 1880.

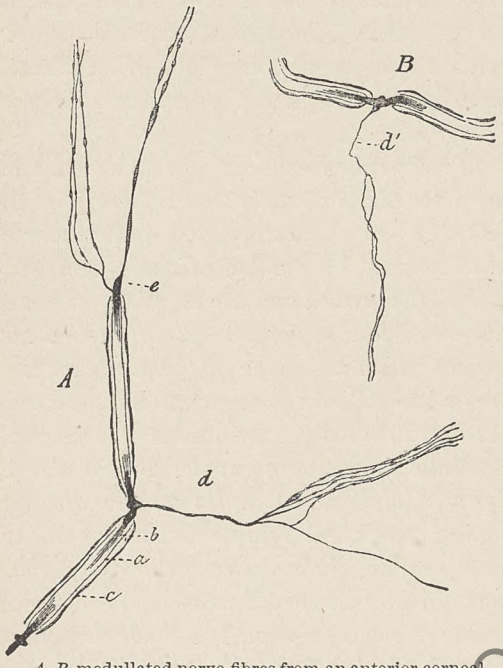
[8] Ranvier: Traité technique d'histologie, 1888.

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others, has been extended by the more recent observations of Dogiel,[1] to whom we are indebted for many additional accurate details regarding the disposition of the nerves within the human cornea. Dogiel has sought the assistance of the newer technique of nerve-staining, and has depended largely upon preparations colored with methylene-blue, which method has yielded such brilliant results in displaying the nerve-endings in other structures.

According to this investigator, about two-thirds of the entire number of nerve-trunks passing into the human cornea, or between forty and fifty, are devoted to the supply of the more anteriorly situated lamellæ, the remainder, or from twenty to thirty, being distributed to the posterior layers. An additional distinction in the distribution of the fibres occurs in the constitution of the primary or *fundamental plexus* formed by the nerve-trunks shortly after entering the substantia propria, since the fundamental plexus situated within the peripheral part of the cornea is derived from the more anteriorly placed nerves, and that of the central area is contributed by the posterior twigs.

Fig. 14.



A, *B*, medullated nerve-fibres from an anterior corneal nerve-trunk; *a*, the peripheral part; *b*, the central fibre of the axis-cylinder; *c*, the medullary substance; *d*, *d'*, nerve-fibrils which pass off from the larger fibre at a node of Ranvier and break up into ultimate fibrillæ; at *e* the central fibre of the axis-cylinder loses its medullary coat and proceeds as minute varicose fibrillæ. Methylene-blue staining. (Dogiel.)

The constituents of the nerve-trunks during their course through the corneal tissue, before losing their medullary substance, give off delicate non-medullated fibres at the constrictions marking the nodes of Ranvier; the fibres so given off soon break up into their component varicose fibrillæ, and are distributed to the various lamellæ of the substantia propria through which the larger nerve-trunk passes.

In addition to the lateral twigs which spring from the main nerve-stem at various levels, *perforating branches* ascend through the anterior corneal lamellæ as far as the epithelium, beneath which tissue they form the *subepithelial plexus*. Since the portions of the subepithelial plexus which these

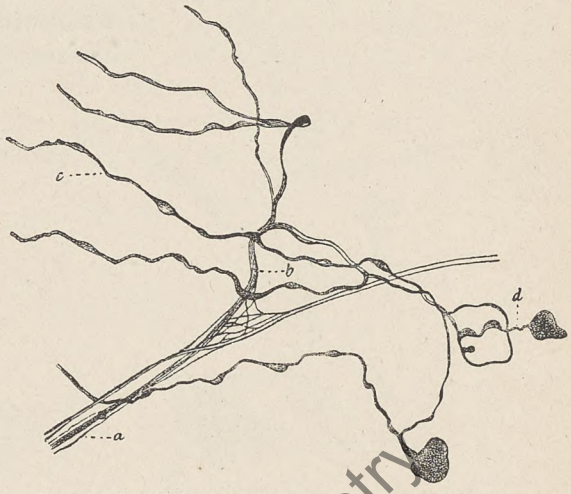
[1] Dogiel: Die Nerven der Cornea des Menschen, Anatom. Anzeiger, Bd. v., No. 16, 1890.

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ascending branches contribute correspond to the portions of the fundamental plexus from which they spring, it follows that the nerve-fibres composing the peripheral parts of the subepithelial net-work are derived from the anterior trunks, while those of the central part proceed from the posterior stems.

The terminations of the perforating twigs composing the subepithelial plexus bear a twofold relation to the anterior corneal epithelium. A few fibres directly pass towards the epithelium and break up into fibrillæ which penetrate between the cells and bear conspicuous round or pyriform terminal *end-bulbs*. (Fig. 15.) A second set of fibres ascend from the subepithelial plexus into the epithelium, among the elements of which they ramify as terminal fibrillæ, and constitute the so-called *intra-epithelial plexus*. The older descriptions of a dense net-work of communicating nerve-fibrillæ existing between the epithelial cells formed by the union of the ultimate nervous threads are not substantiated by the more accurate recent investigations, the presence of such terminal net-works being not only doubtful in regard to the corneal tissue, but likewise in opposition to the conclusions concerning nerve-terminations in general, as based upon the advances made in the more intimate knowledge of the final disposition of nerve-filaments.

Fig. 15.



Termination of the nerves in the anterior part of the cornea.—*a*, twig from an anterior corneal nerve-trunk; *b*, perforating branch; *c*, part of subepithelial plexus; *d*, intra-epithelial fibrillæ ending in terminal plates. Methylene-blue preparation. (Dogiel.)

The observations by Dogiel on nerves stained with methylene-blue agree with those of Feist,[1] and show that the axis-cylinders of the corneal fibres consist of an intensely colored central fibre surrounded by a less deeply tinged envelope,—Feist's peripheral axis-cylinder substance. The ultimate elements of the axis-cylinders of the more robust fibres are traced as delicate varicose fibrillæ, which pass with many tortuosities to their final distribution.

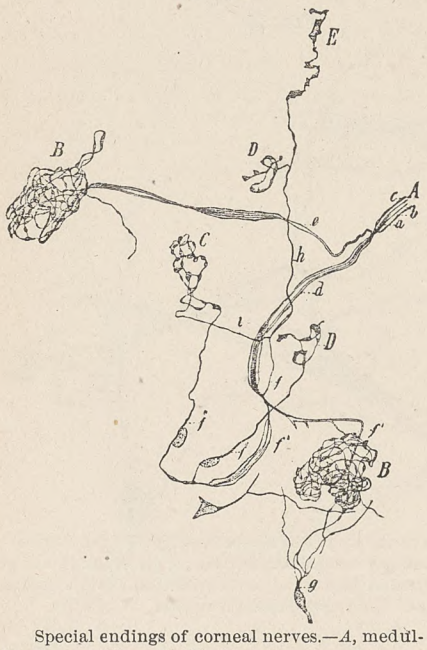
The terminal fibres of the corneal nerves are connected with various forms of end-organs, among which intricately wound ball-like *convolutions*, less closely contorted *hooks* and *loops*, and irregularly quadrate *plates* are

[1] Feist: Ueber die vitale Methylenblaufärbung markhaltiger Nervenstämme, 1889.

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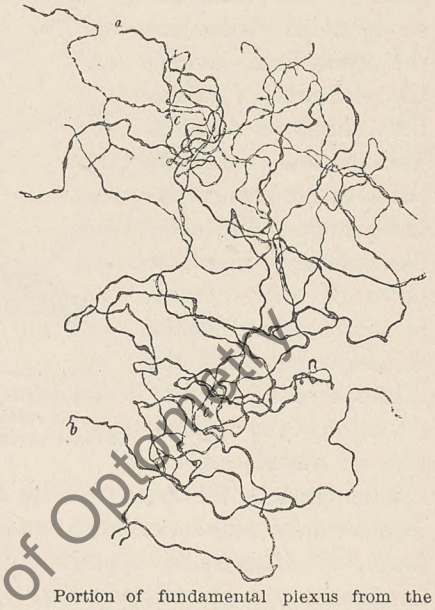
conspicuous. The spherical convolutions consist of aggregations of the greatly contorted and closely intertwined non-medullated terminal fibrillæ, which thus form conspicuous objects at the extreme periphery of the cornea within a zone from .5 to 1.5 millimetres in width next the limbus. The terminal hooks, which occur within the same area, are formed by less closely wound fibrillæ derived by the repeated division of the larger bundles; they present variations in their details, some being sharply turned, while others are bent in more gradual curves. In addition to terminal convolutions and hooks which are found especially within the periphery beneath the anterior limiting membrane, the

FIG. 16.



Special endings of corneal nerves.—*A*, medullated nerve-fibres dividing into two branches, one of which terminates in the convolution *B*, the other breaks up into three twigs, *fff''*; *f* subdivides into *h* and *i*; *h* ends in a loop (*D*) and a hook (*E*); *f'* passes into the terminal convolution *B*; *b''* splits into smaller fibrillæ; *g*, terminal fibrillæ of neighboring twig, which take part in forming the convolution; *a*, *b*, parts of the axis-cylinder; *C*, medullary substance. Methylene-blue preparation. (Dogiel.)

FIG. 17.



Portion of fundamental plexus from the periphery of the anterior layers of the cornea.—*a*, *b*, twigs derived from different corneal nerves; *c*, *c'*, areas in which *a* and *b* form an especially rich plexus. Methylene-blue preparation. (Dogiel.)

terminal fibrillæ within this zone are associated with special endings in the form of irregularly quadrate or spade-like plates; these are usually connected with varicose fibrillæ which pass off as non-medullated twigs, derived from the fundamental plexus or from the perforating branches. The existence of the peculiar club-shaped and forked nerve-endings described by Brand[1] in the human cornea is very doubtful, and, indeed, has been directly denied by Dogiel; the pictures obtained by Brand seem to be due

[1] Brand: Die Nervenendigungen in der Hornhaut, Archiv f. Augenheilkunde, Bd. xix., 1888.

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to imperfectly stained preparations, since he declares the rami perforantes to be the terminal fibrils of the corneal nerves, and denies the presence of nervous filaments both beneath and within the epithelium.

The plexuses within the substantia propria are formed by the ramifications of the twigs given off at various levels from the perforating trunks and of the terminal pencils of fibrillæ into which the nerve-trunks break up. In successful preparations, five or six distinct layers of interwoven fibrils occur within the substantia propria in different planes, the plexuses spreading out between the strata of fibrous tissue.

The points of meeting of the fibres supplying the corneal stroma are usually marked by angular areas outlined as well as traversed by the interlacing fibrils which join one another at acute angles of varying magnitude. Within these nodal points nuclei are often to be distinguished, which, however, belong to the delicate investing sheaths, and not to ganglion-cells, as formerly maintained by some authorities.

Fig. 18.



Portion of fundamental plexus of anterior layers of the cornea. Gold preparation.—*n*, *n*, nodal points. Magnified 120 diameters.

The fibrillæ constituting the fundamental plexuses of the substantia propria are distinguished by the remarkable zigzag course which they pursue after their liberation from the larger nerve-fibres traversing the corneal tissue. The distribution of the fibrillæ, furthermore, is not uniform, since at certain points they become tortuous to an unusual degree, two, three, or even more fibrillæ taking part in the production of an area which becomes conspicuous on account of the elaborate windings of the terminal nervous threads. (Fig. 17, *c*, *c'*.)

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The question as to the relations of the terminal nerve-fibrillæ to the corneal corpuscles has claimed much attention and elicited no little disagreement of opinion among observers. Kühne, Königstein, Ciaccio, Waldeyer, and others have accepted a more or less direct connection between the fibrillæ and the protoplasm of the corneal cells, while Hoyer, Klein, Schwalbe, and others regard such continuity as only apparent. Dogiel gives very positive testimony in opposition to the assumed continuity of these structures, which conclusion fully accords with the views of the writer. The fact that the nerve-fibrillæ forming the various interlacements, which collectively constitute the fundamental plexus, lie within the interfascicular clefts, and hence closely associated in position with the corneal corpuscles, renders the determination of the exact relation between the cells and fibrillæ often a matter of difficulty and uncertainty, but critical examination usually convinces that contiguity and not continuity exists between these structures, and that the relations of the nerve-fibrillæ to the connective-tissue elements within the corneal stroma do not present a remarkable exception to the relations of such structures elsewhere.

THE SCLERA.

The sclerotic coat contributes the posterior four-fifths of the dense fibrous tunic, and is largely instrumental in maintaining the form of the eyeball; at the sclero-corneal juncture the sclerotic tissue is directly continuous with that of the cornea in front. This coat is imperfect in the vicinity of the posterior pole, owing to the passage of the optic nerve through the fibrous tunic, at this point the sclera being represented by the net-work of interlacing fibrous bundles which constitutes the *lamina cribrosa*, through the interstices of which the optic fibres escape in their course from the interior of the eye to the brain. The sclerotic is additionally pierced by blood-vessels and nerves; those constituting the short ciliary group enter close to the optic nerve, those forming the long ciliary group passing obliquely through the sclera a few millimetres farther forward, while the large vorticose venous trunks make their exit near, but slightly behind, the equator. The anterior ciliary vessels traverse the scleral tissue a short distance posterior to the corneal limbus.

The sclera is thickest in the immediate neighborhood of the optic nerve, at a point about two and a half to three millimetres within and about one millimetre below the posterior pole of the eyeball. In this locality the fibrous tunic measures about one millimetre in thickness, gradually becoming thinner towards its anterior boundary. The thinnest part of the sclera corresponds to the zone covered by the tendons of the ocular muscles, which lies about seven millimetres behind the limbus; beneath the tendons the coat measures only about .35 millimetre. After receiving the expanded insertions of the recti muscles, the anterior segment of the sclerotic increases slightly in thickness, and at the junction with the cornea measures approximately .6 millimetre. The bluish tint of the sclerotic coat in children de-

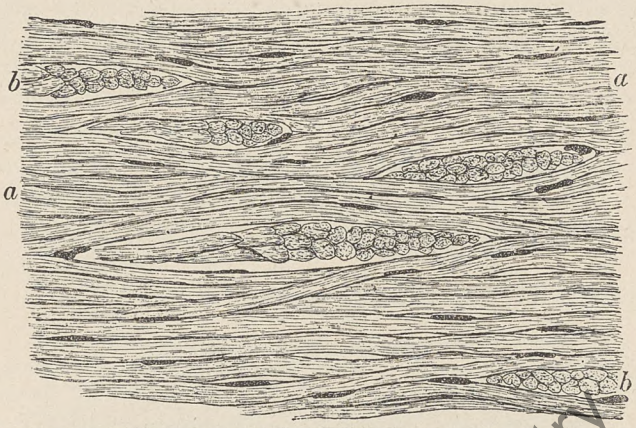
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pends upon the pigmented tissue of the underlying choroid showing through the partially translucent, thin, immature fibrous tunic of the young eye; the yellowish tint observed in old age, on the contrary, is due to accumulations of adipose tissue.

The sclera resembles the cornea in its general structure in being made up of a framework of closely united interlacing bundles of white fibrous tissue, throughout which extends a system of intercommunicating lymph-spaces in which lie the connective-tissue cells, the *sclerotic corpuscles.*

The white fibrous tissue of the sclera yields gelatin on boiling, and is

FIG. 19.



Section of sclera showing the component fibrous tissue (*a*) arranged as interlacing lamellæ; in the clefts between the bundles lie the scleral cells; *b, b,* obliquely cut bundles of circularly disposed fibres. Magnified 480 diameters.

arranged in bundles disposed principally in two general directions, equatorially and meridionally, although the individual fibrous bands interlace with one another at all angles. In the vicinity of the corneo-scleral juncture the equatorial fibres are unusually well developed, while posteriorly the meridional ones preponderate. The scleral bundles contain numerous elastic fibres, which are particularly rich within the inner strata of the coat, especially around the points of passage of the vessels and nerves.

The fibrous bundles received from the insertions of the straight ocular muscles blend principally with the meridional fibres of the sclerotic; those from the oblique muscles mingle particularly with the equatorial bundles; in both cases, however, they soon leave the outer surface of the sclera to dip deeply into and become intimately united with the scleral tissue. (Löwig.[1])

The tissue-spaces within the sclerotic coat resemble those of the cornea, but are smaller, less regularly disposed, and less generously provided with an elaborate system of minute connecting canals, the canaliculi. In profile

[1] Löwig: Beiträge zur Morphologie des Auges, Leipzig, 1858.

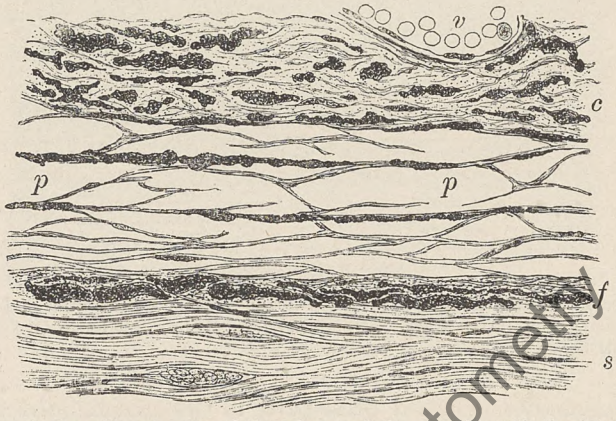
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they appear as lenticular clefts between the interlacing bundles of fibrous ground-substance.

The cells occupying these spaces—the *scleral corpuscles*—in general resemble those of the cornea, and occupy the walls of the spaces; they do not, however, present the extended and richly branched outlines of the corneal cells. Migratory leucocytes—the *wandering cells*—are also occasionally observed within the juice-canals of the sclera. The system of lymph-spaces of the sclerotic coat is, as a whole, less well developed than that of the cornea, with which it stands in free and direct communication at the limbus.

In addition to the usual plate-like corpuscles and the occasional wandering cells included within the lymph-spaces, the sclerotic coat contains pigmented connective tissue cells. These occur in profusion within the inner-

FIG. 21.



Section through the adjacent parts of the sclera and the choroid, with the intervening supra-choroidal space.—*s*, fibrous tissue of the sclera, the innermost pigmented layer of which constitutes the *lamina fusca*, *f*; *p*, the supra-choroidal space traversed by the loose reticulum formed by the trabeculæ; the latter are invested in places by the pigmented cells; *c*, outer zone of the choroid; *v*, partial section of a choroidal vessel. Magnified 480 diameters.

most stratum, where they contribute the color which distinguishes the *lamina fusca* as a dark-brown layer immediately next the supra-choroidal space, the cleft separating the sclera from the choroid. The inner surface of the pigmented layer, which constitutes the outer wall of the space just mentioned, is clothed with endothelium continuous with the covering of the fibrous trabeculæ traversing the cleft as well as the outer surface of the choroid.

Pigmented cells also occur within the sclera in the vicinity of the corneal margin, around the optic entrance, and along the canals transmitting the perforating blood-vessels and nervous trunks. The pigmented elements occurring in these localities present the usual appearances of irregularly stellate connective-tissue cells in which the protoplasm has become more or less filled with the colored particles. The nuclei generally remain

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uninvaded, and appear as light ovoid areas, in sharp contrast to the surrounding deeply colored cell-bodies.

The outer surface of the sclerotic coat is also covered throughout its greater extent, from the insertion of the ocular muscles to the sheath of the optic nerve, with a layer of endothelium which constitutes the lining of the inner wall of the episcleral lymph-sac, or space of Tenon, this latter space being included between the capsule of Tenon without and the sclerotic within.

At the position of the optic nerve, the sclerotic tissue becomes directly continuous with the fibrous tissue composing the external or dural sheath of the nerve; upon the outer surface of this sheath the endothelium covering the eyeball is reflected for some distance to form the inner lining of the supra-vaginal lymph-space. The external surface of the sclera is roughened by the attachment of numerous fibrous trabeculæ which traverse the peri-ocular space to reach the capsule of Tenon, which forms its outer wall.

The Blood-Vessels of the Sclera.—The vascular structures of the sclerotic coat naturally fall within two groups:

1. The blood-vessels which perforate the sclera in their passage to the more deeply lying uveal tract;

2. The blood-vessels of the sclera which are concerned in supplying its tissue.

The vessels constituting the first group, which far exceed in size and importance those distributed directly to the fibrous tunic, are represented by three sets,—(*a*) those piercing the anterior portion of the sclera, as the branches of the anterior ciliary vessels; (*b*) those passing out near the equator of the eyeball, as the large venæ vorticosæ; and (*c*) those penetrating the posterior region of the sclerotic coat in the vicinity of the optic entrance, as the long and the short posterior ciliary arteries. These vessels during their passage through the fibrous coat give off no branches directly distributed to the sclera.

The especial vascular supply of the sclera is exceedingly meagre, consisting, for the most part, of a few twigs given off from the wide-meshed *episcleral net-work*, which ramify within the more superficial strata of the tunic. The episcleral net-work itself is formed by the delicate branches contributed by both the anterior and the posterior ciliary arteries, those from the former being of most importance.

In the immediate vicinity of the position at which the optic nerve pierces the fibrous tunic of the eyeball the short ciliary arteries give off a few small twigs to the sclera; these vessels unite within this tunic to form an encircling anastomosis,—the *circulus Zinnii*,—from which minute branches extend towards the dural sheath of the nerve and join with the arterioles supplying that envelope, thus establishing a communication between the branches of the central retinal and the ciliary vessels.

The small veins which collect the blood from the anterior part of the extended tract provided for by the episcleral net-work become tributaries

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of the anterior ciliary veins; those draining the equatorial zone of the sclera empty into the large venæ vorticosæ, while posteriorly the minute venous radicles from the sclera and the optic nerve join to form the short ciliary veins.

The *lymphatics* of the sclera are represented by the intercommunicating cell-spaces alone, distinct lymph-vessels being wanting. The system of juice-channels being less developed than that of the cornea, the fluids within the former pass freely into the corneal spaces. The lymph-clefts within the sclera in the immediate neighborhood of the angle of the anterior chamber stand in closest relation with the spaces of Fontana, as emphasized by the investigations of Staderini; through their agency, therefore, it is probable that lymph-streams are established towards the more capacious channels within the corneal stroma, as well as towards the lumen of the contiguous veins.

The *nerves* of the sclera may be grouped, like its blood-vessels, into perforating trunks destined for the supply of other structures, and those distributed to the scleral tissue itself. These latter—by no means numerous—ramify principally within the more superficial layers of the coat, being derived, according to the observations of Königstein,[1] as minute twigs from the ciliary nerves as these pass forward between the sclerotic and the choroid coat. The delicate branches so given off soon break up into finer bundles of axis-cylinders, which terminate in highly tortuous and intricately coursing ultimate fibrillæ between the fibrous fasciculi, in a manner somewhat resembling the nerve-endings within the central parts of the corneal stroma.

THE SCLERO-CORNEAL JUNCTURE.

The transition of the dense opaque tissue of the sclera into the beautifully transparent structure of the cornea marks the outer boundary of a region of especial interest, in which four important portions of the eye—the cornea, the sclera, the iris, and the ciliary body—meet. The conspicuous differences between the scleral and the corneal portions of the fibrous tunic depend upon physical rather than morphological variations, since, as already seen, the structural elements and their general plan of arrangement closely correspond.

The tissue of the sclera and the contained lymph-spaces are directly continuous with those of the cornea, and while the scleral spaces are smaller and the circularly disposed bundles of fibrous tissue are particularly well developed, there is much less histological differentiation at the zone of transition than might be expected from the sharply defined macroscopic changes marking the juncture.

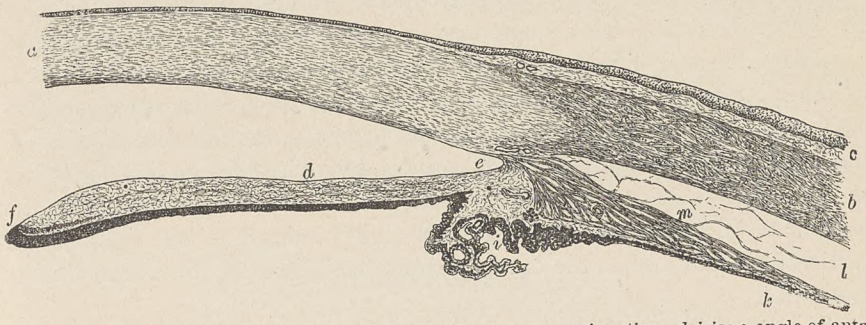
Examination of meridional sections shows that the scleral tissue extends somewhat farther forward at the anterior and posterior borders of the coat

[1] Königstein: Ueber die Nerven der Sclera, Archiv f. Ophthalmologie, Bd. XVII., 1881.

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than at the intervening levels, the projection of the outer boundary passing farther towards the anterior pole than the inner process. In consequence of this arrangement the corneal margin is received within the recess between the external and internal *scleral processes* in a manner suggesting the often quoted relation of a watch-crystal to its frame.

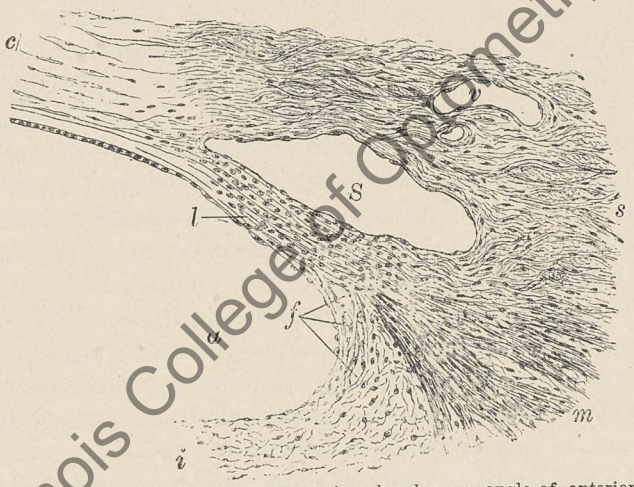
FIG. 22.



Meridional section of ciliary region.—*a*, cornea; *b*, sclera; *c*, conjunctiva; *d*, iris; *e*, angle of anterior chamber; *f*, pupillary margin of iris; *i*, ciliary processes; *k*, ciliary ring; *l*, artificial separation between choroid and sclera; *m*, ciliary muscle. Magnified 23 diameters.

The connections of the inner scleral process are of especial interest on account of their important relations to the structures lying at the anterior angle of the ciliary region where the cornea, the iris, and the ciliary muscle meet. The anterior and external border of the inner scleral process marks

FIG. 23.



Section through the lateral wall of the anterior chamber.—*a*, angle of anterior chamber; *S*, Schlemm's canal; *v*, one of the adjacent scleral veins; *c*, corneal tissue; *s*, scleral tissue; *l*, beginning of the pectinate ligament; *f*, spaces of Fontana; *i*, iris; *m*, ciliary muscle. Magnified 70 diameters.

the position of a conspicuous circular channel which surrounds the limbus corneæ and lies close to the angle of the anterior chamber; this is the canal of Schlemm, an annular venous sinus possessing intimate relations to the anterior lymph-spaces of the eye.

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The *canal of Schlemm* (sinus venosus iridis, sinus venosus Schlemmii, circulus venosus ciliaris), as seen in meridional sections, usually presents a single lumen, elliptical or pyriform in outline, which measures .30 to .34 millimetre and .045 to .050 millimetre in its longest and shortest diameters respectively; not infrequently, however, the lumen of the canal is broken up into two, or even three, compartments by the presence of trabeculæ. This subdivision, however, is usually limited to small portions of the tube, the lumen becoming again single beyond the position of the bridging bands.

The outer wall of Schlemm's canal is formed by the dense scleral stroma; its inner boundary, on the contrary, is composed of a peculiar spongy reticulated fibro-elastic lamella, which appears to be the anterior continuation of the inner scleral process, but which really is derived, as shown by Angelucci,[1] as an extension of the choroidal tract. It is intimately united with the membrane of Descemet anteriorly, and closely related to the ligamentum pectinatum iridis and to the outer or meridional fibres of the ciliary muscle internally.

The *ligamentum pectinatum iridis* consists of an annular prismoidal mass of spongy tissue, composed of interlacing trabeculæ derived from the splitting up of the periphery of the membrane of Descemet; it occupies the angle of the anterior chamber, and unites the iris, the ciliary muscle, and the inner corneal border. Its inner surface, next the anterior chamber, is concave, and stretches between the membrane of Descemet and the ciliary border of the iris. The pectinate ligament of man represents, according to Iwanoff and Rollett,[2] a structure which in many ruminants appears as a series of conical processes extending from the iris towards the cornea. The posterior border of the pectinate mass within the human eye abuts against the root of the iris; its external and longest side is intimately associated with the ciliary muscle, the posterior part of this surface being in close relation with the origin of the meridionally disposed muscular fibres. The posterior layer of the substantia propria at the corneal margin leaves the membrane of Descemet to become directly continuous with the scleral stroma constituting the outer wall of Schlemm's canal, the interspace resulting from this divergence being occupied by the anterior extremity of the reticulated continuation of the inner scleral process. This latter tissue, while closely joined to the scleral coat, is genetically a part of the uveal tract, and must be regarded as belonging to the choroid rather than to the sclerotic coat. The intimate relations existing between the membrane of Descemet and its endothelium and the anterior limits of the vascular tunic of the eye are founded on their primary common genesis and early continuity, in recognition of which, as already stated, these strata are regarded as constituting the *pars uvealis corneæ*.

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[1] Angelucci: Ueber Entwickelung und Bau des vorderen Uvealtractus der Vertebraten, Archiv f. mik. Anatom., Bd. XIX., 1881.

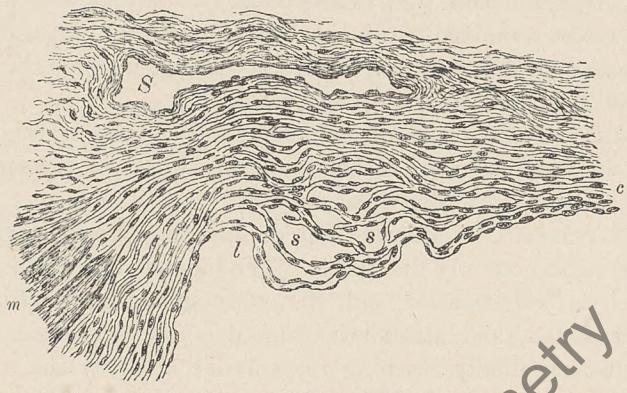
[2] Iwanoff und Rollett: Bemerkungen zur Anatomie der Irisanheftung und des Annulus ciliaris, Archiv f. Ophthalmol., Bd. XV., 1869.

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The peripheral portion of this structure, which the apparent continuation of the inner scleral process may be regarded as forming, sometimes presents a thickened anterior edge, described by Schwalbe[1] as the *boundary ring* of Descemet's membrane. This ring, which in many lower mammals is represented by a well-developed annular bundle of elastic fibres, gives origin to the numerous bands constituting the reticulum of the inner wall of Schlemm's canal, as well as attachment to many trabeculæ taking part in the formation of the pectinate ligament.

The tissue composing the ligamentum possesses the homogeneous elastic character of the posterior limiting membrane of the cornea, from which the trabeculæ are directly continued. As pointed out by Straub,[2] the membrane of Descemet gives origin to two layers, an inner and an outer. The

FIG. 24.



Section through sclero-corneal junction.—*S*, Schlemm's canal; *l*, the relaxed tissue constituting the pectinate ligament, including the interfascicular spaces of Fontana (*s*, *s*); *c*, corneal attachment of trabeculæ of pectinate ligament; *m*, several bundles of the ciliary muscle. Magnified 100 diameters.

former breaks up into an open mesh-work of delicate trabeculæ, from .002 to .007 millimetre in thickness, imperfectly invested by endothelial plates, which pass towards the iris, with which structure they finally blend. The behavior of this tissue when viewed by polarized light demonstrates the identity of its nature with that of the membrane of Descemet, of which it is a part, or at least the direct extension, and not merely ordinary connective tissue. The deeper layer forms connected plates or lamellæ which constitute a cavernous tissue of elastic character: while a small portion of this structure may be traced into the iris, the greater part affords attachment to the bundles composing the ciliary muscle. The interlacing of the bands so derived produces a sponge-like framework which encloses numerous intercommunicating clefts, the *spaces of Fontana*. These spaces are covered with an imperfect endothelial investment, formed by the plate-like elements

[1] Schwalbe: Untersuchungen über die Lymphbahnen des Auges und ihre Begrenzungen, Archiv f. mik. Anat., Bd. VI., 1870.

[2] Straub: Notiz ueber die Ligamentum pectinatum und die Endigung d. Memb. Descemeti, Archiv f. Ophthalmol., Bd. XXXIII., 1887.

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directly continued over the individual trabeculæ from the endothelium of Descemet's membrane.

The spaces of Fontana of the human subject are relatively much less developed than in the eyes of many lower mammals, as the horse, ox, or pig, in which they are of greater size and form a more elaborate system of intercommunicating lacunæ. The spaces in man are mere interfibrillar crevices, small and narrow near the corneal margin, but of larger dimensions in the vicinity of the iris; from the nature of their boundaries they are not completely isolated, but constitute a system of imperfectly walled irregular channels which, in addition to freely communicating with one another, allow the ready entrance of the fluid contents of the anterior chamber. The aqueous humor consequently enters and fills these interfascicular spaces within the tissue of the pectinate ligament. The close contact of the latter with the reticulated inner wall of Schlemm's canal brings the clefts contained within the septal tissue into intimate relations with the spaces of Fontana, an important passage-way for the escape of the intra-bulbar lymph being thus suggested.

The nature of the canal of Schlemm and of the relations of this channel to the anterior chamber has been the subject of repeated investigations which have led to divergent opinions.

In 1869 Schwalbe[1] observed that on injecting Berlin blue into the anterior chamber not only the spaces of Fontana and the adjacent interfascicular clefts became filled with the coloring matter, but likewise the canal of Schlemm, and secondarily the neighboring scleral veins, the injected substance finally reaching the anterior ciliary veins. Schwalbe, therefore, upon the evidence of his experiments, announced the existence of a free communication between the anterior chamber and the anterior ciliary veins, maintaining the connection of the canal of Schlemm with the anterior chamber through the interfascicular and Fontana's spaces on the one hand, and with the scleral and anterior ciliary veins, by means of lateral channels uniting Schlemm's canal with the adjacent scleral veins, on the other. This authority originally regarded Schlemm's canal as an annular lymph-sinus which discharged the fluids received from the anterior chamber into the tributaries of the anterior ciliary veins.

Leber,[2] while admitting the close relation between the anterior chamber and the canal of Schlemm, denied the possibility of injecting non-diffusible substances from the anterior chamber into the canal unless sufficient pressure were employed to rupture the delicate endothelial partition which normally closes the canal. This investigator further declared that diffusible substances alone passed into Schlemm's canal and the ciliary veins when all mutilations were avoided. Leber also combated the opinion that the canal

[1] Schwalbe: Untersuchungen über die Lymphbahnen des Auges und ihre Begrenzungen, Archiv f. mik. Anat., Bd. VI., 1870.

[2] Leber: Studien ueber den Flüssigkeitswechsel im Auge, Archiv f. Ophthalmol., Bd. XIX., 1873.

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was a lymph-space, maintaining that its true nature was that of an annular venous sinus, often represented by a plexus of smaller radicles rather than by a single trunk.

The controversy thus initiated, based as it was upon the directly contradictory results obtained by two eminently skilful observers, naturally attracted much attention; subsequently the desirability of possessing accurate information concerning the nature and relations of Schlemm's canal incited investigators from time to time to renewed studies of the subject, with a view of determining which of the conflicting opinions was correct. Among those accepting Schwalbe's views and supporting them by their experiments, Waldeyer[1] and Heisrath[2] are conspicuous. It is to be noted, however, that the last-named observer, in his later paper,[3] gives only partial allegiance to his older views, and partially, at least, inclines to those of Leber; indeed, Schwalbe[4] himself, apparently, later modified his teaching regarding the nature of Schlemm's canal so far that he accepted its character as a venous channel and no longer maintained that it was purely a lymph-vessel. Rochon-Duvigneaud[5] and Gifford[6] are also investigators who succeeded in filling the canal of Schlemm and its neighboring veins by injection introduced into the anterior chamber.

Those supporting Leber's views, that Schlemm's canal is a venous sinus, and that the anterior chamber does not stand in open communication with the ciliary veins by means of the canal, include Brugsch,[7] Königstein,[8] Angelucci,[9] Morf,[10] Staderini,[11] Merian,[12] and Merkel.[13]

Until very recently, therefore, notwithstanding repeated painstaking

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[1] Waldeyer: in Graefe und Saemisch's Handbuch.

[2] Heisrath: Ueber den Zusammenhang der vorderen Augenkammer mit den vorderen Ciliarvenen, Archiv f. mik. Anat., Bd. xv., 1878.

[3] Heisrath: Ueber die Abflusswege des Humor aqueus, mit besonderer Berücksichtigung des sogennanten Fontana'schen und Schlemm'schen Canales, Archiv f. Ophthalmol., Bd. xxvi., 1880.

[4] Schwalbe: Anatomie der Sinnesorgane, 1887, p. 176.

[5] Rochon-Duvigneaud: Recherches anatomiques sur l'angle de la chambre antérieure et le canal de Schlemm, Archives d'ophthalmol., t. xii., xiii., 1892–93.

[6] Gifford: Weitere Untersuche über die Lymphströme und Lymphwege des Auges, Archiv f. Augenheilkunde, Bd. xxvi., 1893.

[7] Brugsch: Ueber die Resorption körnigen Farbstoffs aus der vorderen Augenkammer, Archiv f. Ophthalmol., Bd. xxiii., 1887.

[8] Königstein: Ueber den Canalis Schlemmii, Archiv f. Ophthalmol., Bd. xxvi., 1880.

[9] Angelucci: Ueber Entwickelung und Bau des vorderen Uvealtractus der Vertebraten, Archiv f. mik. Anat., Bd. xix., 1881.

[10] Morf: Experimentelle Beiträge zur Lehre von dem Abflusswegen der vorderen Augenkammer, Inaug. Dissertation, Winterthur, 1888.

[11] Staderini: Ueber die Abflusswege des Humor aqueus, Archiv f. Ophthalmol., Bd. xxxvii., 1891.

[12] Merian: Versuche ueber die Lymphwege des Auges, Archiv f. Anat. und Physiologie, 1891.

[13] Merkel: Ergebnisse der Anatomie und Entwickelungsgeschichte, Bd. i., 1892, p. 240.

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investigations concerning the behavior of injection-fluids forced into the anterior chamber, no definite conclusions were possible, since the same conflicting testimony existed as did a decade before. It will be noticed, however, that the majority of these investigators gave weight to the view opposing an open communication between the anterior chamber and Schlemm's canal, most of these observers declaring that it was impossible to introduce substances injected into the anterior chamber into the scleral veins by way of the canal.

The appearance of the paper of Gutmann[1] in 1895 gave new and very strong additional support to Schwalbe's claim that it is possible to inject a non-diffusible substance, as Berlin blue, into the scleral veins by way of the canal of Schlemm, since Gutmann's experiments with a large series of human eyes conclusively show that such filling takes place even when the injections are performed under conditions which preclude the occurrence of any mutilation from the employment of undue force or pressure. Gutmann's investigations were so carefully carried out that it is impossible to doubt the conclusive character of their evidence.

Stimulated by these results, which threatened the overthrow of his long-defended views as to the impossibility of injecting the anterior ciliary veins from the anterior chamber, Leber,[2] with the assistance of Beutzen, undertook a series of renewed investigations to furnish additional support of his opinion and to meet the results of Gutmann's observations. Leber and Beutzen avoided the one vulnerable feature of Gutmann's work—the employment of eyes derived from human cadavers, which were therefore not absolutely fresh—by carrying out the injections on eyes which were entirely free from post-mortem change.

His former experiments with carmine and Berlin blue Leber repeated under conditions similar to those originally observed, with almost identical results,—namely, that the carmine passed into the veins by diffusion while the Berlin blue remained behind. On performing injections in repetition of Gutmann's experiments under the conditions emphasized by this writer, —after the partial escape of the aqueous humor,—Leber was astonished to find that the canal of Schlemm and the anterior ciliary veins almost at once became filled with the Berlin blue injected into the anterior chamber under low pressure and with the least possible force. Careful and repeated experiments conclusively demonstrated that the conflicting results of the various investigations during the last fifteen years depended not upon inaccurate observations, but largely upon the degree to which the aqueous humor had escaped before the injection was undertaken. To Leber, therefore, belongs the satisfaction of having thus discovered the principal source of the perplexing discrepancies which have so long existed between the results

[1] Gutmann: Ueber die Natur des Schlemm'schen Sinus und seine Beziehungen zur vorderen Augenkammer, Archiv f. Ophthalmol., Bd. XLI., 1895.

[2] Leber: Die Circulus venosus Schlemmii steht nicht in offener Verbindung mit der vorderen Augenkammer, Archiv f. Ophthalmol., Bd. XLI., 1895.

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of the many able investigators who have busied themselves with the relations of the anterior lymph-paths of the eye.

The exact nature of the communication between the canal of Schlemm and the adjacent interfascicular clefts still remains to be settled, but it may be assumed, as accepted by Leber and Merkel, that intra-ocular fluids and injected substances find a passage into the canal of Schlemm through the minute clefts and stomata between the elements of the endothelial wall of the channel; that an "open communication," in the sense originally maintained by Schwalbe, does not exist will be, we believe, the conclusion of most observers who have carefully studied the histological characteristics of the inner wall of Schlemm's canal.

The relations of the lymph-filled spongy tissue interposed between the anterior chamber and the canal of Schlemm find a close parallel in the arrangement of the tissue of the arachnoidal villi and the sinuses of the dura mater, as seen in the Pacchionian bodies. Just as these structures serve as points of escape for the lymph-fluid of the subarachnoidal space into the venous channels, whereby the equilibrium of the intra-cranial pressure is maintained, so the constant escape of the aqueous humor into the venous channels, by means of the paths afforded by the interfascicular clefts situated at the angle of the anterior chamber, is an important means of maintaining the normal intra-ocular tension.

The venous nature of Schlemm's canal, as constantly maintained by Leber, is now almost universally accepted. Waldeyer, who long held to the lymphatic character of the canal, has recently[1] indirectly announced the relinquishment of his former views in favor of the venous nature of the sinus. The evident correspondence between the relations of the arachnoidal villi and the dural venous sinuses was a potent argument in inducing Waldeyer to accept the venous nature of Schlemm's canal.

The seemingly strong argument which has been so often advanced against considering the canal a venous channel—namely, that the lumen of the canal is usually empty, or at least devoid of blood-corpuscles—loses much of its force when we appreciate the fact, as emphasized by Leber, that the filtration-current continues for some time after death, and, consequently, tends to remove what blood-cells were within the canal during life. It is, however, by no means rare to observe blood-cells still within the canal, such elements being especially present in eyes subjected to fixing solutions immediately after death. Positive testimony as to the occurrence of blood-cells within the canal has been given by a number of observers, among whom are Leber, Heisrath, Königstein, and Rochon-Duvigneaud. Leber found no difficulty in injecting the canal of Schlemm from the scleral veins, but records his failure to cause the injection to pass into the spaces of Fontana or the anterior chamber.

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[1] Gutmann, in the above-cited paper, states his distinct authorization to announce this change in Waldeyer's views.

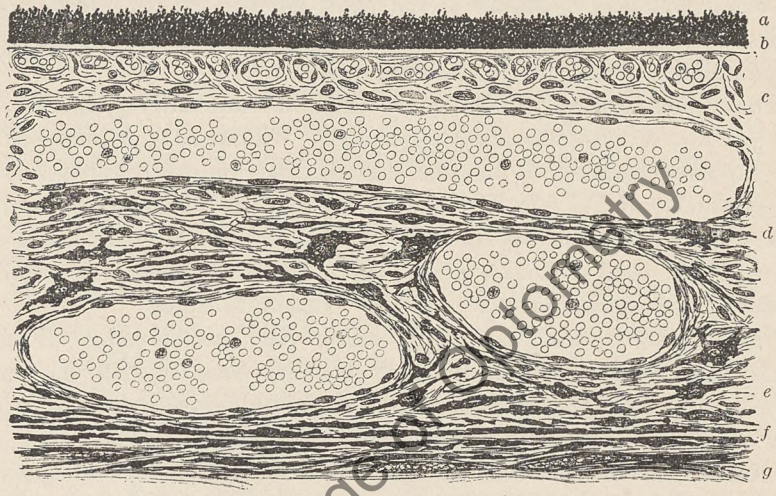
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The canal of Schlemm may therefore be regarded as closely connected with the anterior chamber on the one hand, and in direct communication with the anterior ciliary veins on the other, probably forming, as suggested by Schwalbe, an annular reserve diverticulum for the reception and temporary storage of venous blood when the usual escape of the latter, as afforded by the anterior ciliary veins, is for any reason unduly retarded. The explanation of the fact that the canal of Schlemm, under ordinary conditions, contains little blood is to be sought, according to Schwalbe, in the narrowness (.024 millimetre in diameter) of the vessels connecting the canal with the anterior scleral veins, which renders the entrance of blood into the lateral diverticulum, while passing along these vessels, much less easy than the direct continuance along the veins.

THE VASCULAR TUNIC OF THE EYE.

The middle or vascular coat, frequently also called the *uveal tract*, is distinguished by the number of its blood-vessels and the dark color imparted to it by the pigmented cells which it contains. The tunic is com-

FIG. 25.



Section of the choroid with portions of the adjacent coats.—*a*, retinal pigment; *b*, vitreous membrane; *c*, chorio-capillaris; *d*, layer containing large blood-vessels; *e*, pigmented stroma; *f*, supra-choroidal space; *g*, lamina fusca of the sclerotic. Magnified 335 diameters.

posed of two portions, the *choroidal tract* and the *iris*. The former lines the sclerotic coat from the position of the optic-nerve entrance to the sclero-corneal juncture; the latter diverges a short distance behind the corneal margin to form the conspicuous diaphragm which stretches across the front of the crystalline lens and behind the cornea. The iris divides the space occupied by the aqueous humor into the posterior and the anterior chamber, communication between the two being established through the circular opening occupying the central area of the iris,—the pupil.

The anterior portion of the choroidal tract, extending from the anterior

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margin of the visual part of the retina, or the ora serrata, to the sclero-corneal juncture, presents remarkable specializations which result in the production of a greatly thickened layer; on the outer surface of the latter an important triangular muscular ring—the ciliary muscle—is developed, and on the inner a series of prominent radial projections—the ciliary processes—is formed. It is usual, therefore, to designate the anterior part of the choroidal tract—which includes the triangular area bounded by the sclero-corneal juncture and the sclera externally, the iris internally, and the ora serrata posteriorly—collectively as the *ciliary body;* the entire choroidal tract may be regarded as thus composed of two segments, the *choroid proper*, lying behind the ora serrata, and the *ciliary body*, in front.

THE CHOROID.

While closely applied to the inner surface of the fibrous tunic, the choroid proper is less intimately united to the sclera than might at first sight be supposed, since only at two points—namely, around the optic entrance and at the inner scleral process—are the tissues of the two coats firmly united. The perforating blood-vessels and nerve-trunks passing between the sclera and the choroid afford important additional points of fixation between the two coats. Throughout the remaining extent of the choroid the sclerotic and vascular tunics are separated by the supra-choroidal space, the two being held together by the intervening bands of fibrous tissue which bridge this cleft and form a loose mesh-work of trabeculæ attached to its inner and outer walls. The outer surface of the choroid is roughened by the attachment of these fibrous trabeculæ; its inner surface, on the contrary, is smooth and so intimately related to the external pigmented layer of the retina that the latter very frequently adheres to the choroid rather than to the remaining parts of the nervous tunic when the latter is removed from the eye.

The color of the choroid after death varies from a reddish to a dark brown, depending upon the amount of pigment contained within its cells. In thickness, the coat presents a gradual reduction from the posterior pole, where in the vicinity of the optic entrance it measures from .05 to .08 millimetre, to the neighborhood of the ora serrata, at which point it is thinnest, being little more than half as broad as in its posterior segment. At the equator of the eyeball the relative thickness of the sclera, the choroid, and the retina is respectively about as sixteen, five, and seven.

The *structure of the choroid* includes, essentially, a more or less compact connective-tissue stroma supporting numerous blood-channels which vary in size from the large and conspicuous emergent veins to minute capillaries. The arrangement of the blood-vessels largely accounts for the peculiarities which distinguish the layers into which the choroid is conventionally divided. These are three in number:

1. The layer of choroidal stroma containing large blood-vessels.
2. The layer of dense capillary net-works,—the chorio-capillaris.

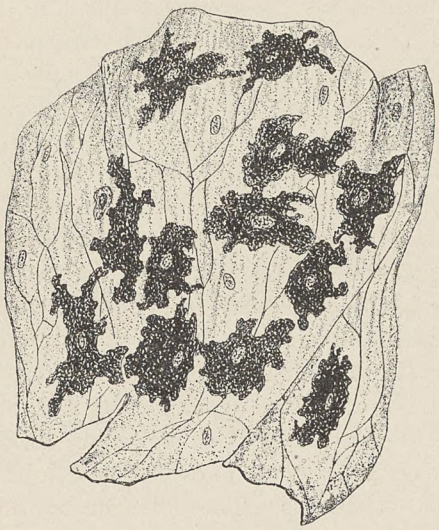
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3. The homogeneous glassy lamina, or vitreous membrane.

The delicate stratum of spongy tissue connecting the outer surface of the choroid and the inner aspect of the sclera, the *lamina supra-choroidea*, by some authorities is regarded as a fourth, and external, layer.

The *lamina supra-choroidea* consists of some half-dozen irregular sheets of broad trabeculæ which join one another at various acute angles to produce a delicate reticulum, the contained meshes of which form a system of intercommunicating lymphatic clefts collectively known as the supra-choroidal lymph-space.

Fig. 26.



Surface view of a fragment of the lamina supra-choroidea: the flat pigmented connective-tissue cells lie upon the elastic lamellæ. Magnified 335 diameters.

The propriety of regarding the supra-choroidal cleft as a lymph-space has been questioned by Langer,[1] who considers it the result of the necessity of a loose connection between the adjacent surfaces of the sclera and the choroid in order to admit of the play of the choroid in response to the contractions of the meridional fibres of the ciliary muscle. While admitting this purpose of the loose connection between the two tunics, there seems no adequate reason to ignore the direct testimony of Schwalbe[2] and of Michel[3] as to the communication of the supra-choroidal space with other lymph-tracts. The arrangement of the lymphatic capillaries within the choroidal stroma, as described by Alexander,[4] and the well-recognized universal close relations of interfascicular clefts to the lymphatic system in other structures, are additional considerations for regarding the perichoroidal space as a lymph-channel.

The membrane-like trabeculæ or partitions are made up of a framework composed of interlacing elastic fibres, upon the surface of which lie numerous flattened, irregularly branched, pigmented connective-tissue cells. These elements appear as conspicuous stellate or plate-like bodies, the deeply colored

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[1] Langer: Beiträge zur normalen Anatomie des menschlichen Auges, Sitzungsberichte d. k. Akad. d. Wissensch. in Wien, Bd. xcix., 1890.

[2] Schwalbe: loc. cit.

[3] Michel: Beiträge zur Kenntnisse der hinteren Lymphbahnen des Auges, Archiv f. Ophthalmol., Bd. xviii., 1872.

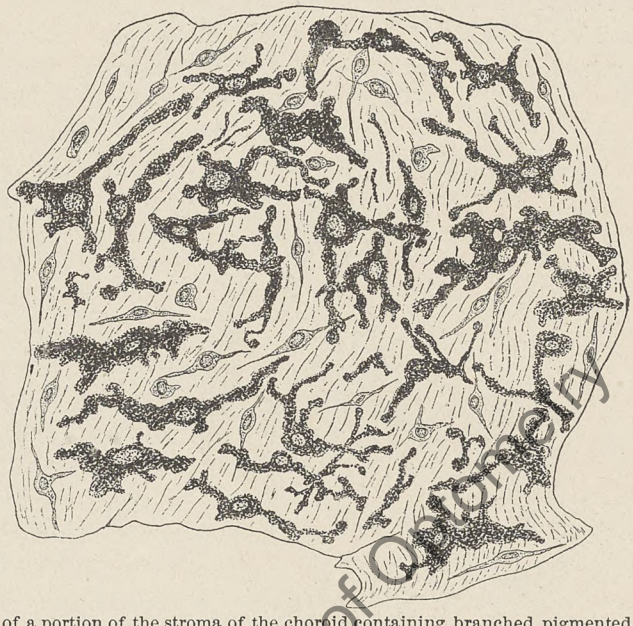
[4] Alexander: Ueber die Lymphcapillaren der Choroidea, Archiv f. Anat. u. Physiol., Anat. Abth., 1889.

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protoplasm of which is relieved by clearer ovoid areas denoting the position of the uninvaded nuclei. In places where the cells are grouped their form approaches more closely that of the typical endothelial plate, possessing a distinctly polyhedral outline.

These plates not only cover the surfaces of the membranous trabeculæ, but provide a more or less perfect endothelial investment for the inner choroidal and the outer scleral wall of the space, as satisfactorily demonstrated by the application of silver staining. As pointed out by Hache,[1] however, the cells covering the scleral surface of the space much more closely approach the endothelial type than those occupying the inner wall,

FIG. 27.



Surface view of a portion of the stroma of the choroid containing branched pigmented cells between which lie the non-pigmented connective-tissue elements. Magnified 335 diameters.

the latter retaining to a greater extent their characteristics as isolated connective-tissue corpuscles. At those points where the perforating vessels and nerves cross the supra-choroidal space the reticulated tissue becomes condensed and contributes sheaths which surround the trunks during their passage, the pigment-cells sometimes forming accompanying chains of colored protoplasmic figures.

The *choroidal stroma* or ground-substance consists of connective-tissue lamellæ closely interwoven with one another and intimately related to the blood-vessels which they support. The structural elements of the stroma

[1] Hache: Sur la structure de la chorioide et sur l'analogie des espaces conjonctifs et des cavités lymphatiques, Compt. rend. hebd. d. s. de l'acad. d. sciences, tome CIV., 1887.

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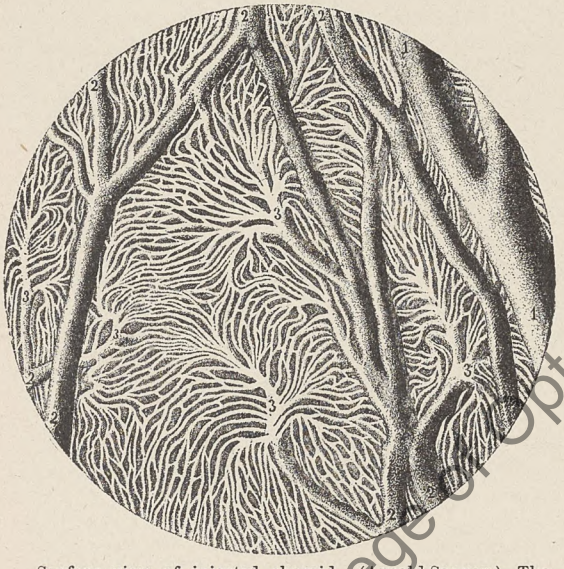
include delicate fibrous bundles, numerous elastic fibres, stellate pigmented and endothelioid cells. These are so closely united with the walls of the blood-channels that considerable firmness is given to the choroid, especially its outer zone.

The stroma layer, with the large blood-vessels, constitutes the greater part of the choroid; the freely branching arterial and venous trunks, taking their course within the supporting tissue made up of closely united connective-tissue lamellæ, elastic fibres, and pigment-cells, appear as lighter-colored channels within the darker surrounding stroma.

The largest vessels occupy the most superficial or outer stratum of the choroidal stroma, those next in size the middle layer, while the smallest approach the inner boundary of the choroid, where they constitute the dense capillary net-work known as the *chorio-capillaris*.

The most conspicuous of the large superficial blood-channels are the four great venous trunks, the *venæ vorticosæ*, which mark upon the outer surface of the choroid, at points about equidistant within the equatorial plane, the foci towards which the smaller tributaries of each quadrant converge to form the remarkable venous whorls occupying the outer layers of the choroidal stroma. Not infrequently one or more of these large receiving veins is represented by two vessels separated often by some distance, this disposition resulting in the presence of five or six venæ vorticosæ.

FIG. 28.



Surface view of injected choroid. (Arnold-Sappey.)—The smaller venous radicles converge in the peculiar manner to form the larger trunks (3, 3), which in turn are tributaries of still larger veins (2, 2); 1, 1, veins of greater diameter.

The blood carried off by these vessels is collected not only from the choroid proper, but also from the ciliary body and the iris. The radially disposed and but slightly tortuous tributaries coming from the latter sources pass backward in their course to join the large collecting veins. On approaching the equator of the eyeball, and still farther towards the posterior pole, the venous radicles assume a progressively more and more arched course in order to reach the vorticose veins, in consequence of which disposition the characteristic whorled arrangements are produced. After receiving their tributaries, the venæ vorticosæ cross the supra-choroidal

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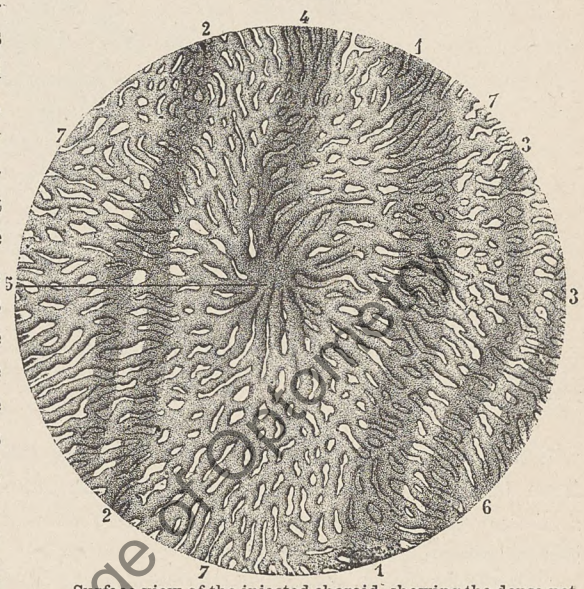
lymph-space and pierce the sclera obliquely and backward, accompanied by an imperfect envelope continued from the lamina supra-choroidea.

The veins of the choroid are usually provided with a perivascular lymph-sheath formed by the addition of an enveloping layer of endothelial plates; this sheath is strengthened externally by an adventitious coat composed of concentrically disposed connective-tissue lamellæ in which longitudinal fibres are well marked. The adventitia is relatively better developed on the smaller than on the larger veins.

The arteries of the choroid, in addition to the well-marked circularly disposed muscle, possess longitudinal bundles of muscle-fibres; these axial bands in some instances, particularly in the vessels supplying the posterior segment, are connected by a net-work of smaller fasciculi.

The layer containing the larger veins is separated from that supporting the capillary reticulum by means of a narrow *boundary zone*, about .010 millimetre in thickness, consisting of a close felt-work of elastic fibres and sparingly distributed connective-tissue cells. The latter are usually entirely devoid of pigment, or, at most, but slightly tinted. The boundary zone, therefore, is to be regarded not as a distinct portion of the choroid, but rather as the innermost part of the stroma layer, which is unusually condensed and slightly pigmented.

FIG. 29.



Surface view of the injected choroid, showing the dense net-work of the chorio-capillaris. (Sappey.)—In the centre of the field the converging capillaries form one of the venous radicles lying within an external plane.

In the eyes of many animals (horse, cow, sheep) the boundary zone possesses wavy bundles of connective tissue, to the peculiar arrangement of which is due the metallic reflex sometimes seen in such eyes; this shining structure constitutes the *tapetum fibrosum*, as distinguished from the iridescent *tapetum cellulosum* of the carnivora, which latter depends upon the presence of several layers of plate-like cells containing innumerable small crystals.

The *chorio-capillaris* (membrane of Ruysch), the capillary zone of the choroid, occupies the inner portion of the vascular coat, being separated from the nervous tunic by the delicate vitreous membrane alone. The capillary net-work, derived from numerous twigs given off from the short

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posterior ciliary arteries, lies embedded within an apparently homogeneous ground-substance, devoid of pigmented elements, which fills the inter-capillary meshes. The exact nature of this matrix is uncertain, but it may be regarded as a modified connective tissue of soft consistence, which stands, probably, according to the investigations of Alexander,[1] in close relation with the more definite lymph-paths and the perivascular lymph-sheaths surrounding the larger venous trunks.

In extent the chorio-capillaris corresponds closely with the visual portion of the retina, for the nutrition of the outer non-vascular layers of

FIG. 30.



Surface view of the choroid seen from the inner side.—*a*, *a*, choroidal stroma separating larger blood-vessels (*b*, *b*); *c*, *c*, the more superficial capillary net-work of the chorio-capillaris. Magnified 115 diameters.

which this capillary net-work seems to be especially designed. It extends from the optic entrance, around which anastomosis between the choroidal and the retinal system of vessels takes place, as far forward as the ora serrata, at which point it abruptly terminates.

The *vitreous membrane*, glassy lamina, or membrane of Bruch, constitutes the inner boundary of the choroid, separating the chorio-capillaris from the outer retinal layer. This lamella appears as a delicate homogeneous, structureless zone, measuring but .002 millimetre in thickness, which is intimately united with the capillary layer on the one hand, and supports the retinal pigment of the retina on the other; patches of the pigment not infrequently adhere to the surface of the glassy lamina, thereby producing polygonal tracings. The use of macerating reagents sometimes effects the separation of the lamella into two layers, the outer of which appears finely reticular.

[1] Alexander: Ueber die Lymphcapillaren der Chorioidea, Archiv f. Anat. u. Physiol., Anat. Abth., 1889.

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Sattler[1] regards this separation as indicating the normal constitution of the vitreous membrane of two distinct lamellæ, an inner homogeneous and an outer composed of a delicate reticulation of interlacing trabeculæ of varying thickness. According to this author, the two layers are always separable in the eyes from young subjects, but very imperfectly so in those from old individuals. Kerschbaumer[2] also accepts this differentiation of the seemingly structureless vitreous membrane into an outer and an inner lamella.

The *nerves* of the choroid are derived from twigs which are given off from the long and short ciliary nerves as these pass between the fibrous and vascular tunics in their course to the ciliary body, from which filaments proceed to the cornea and the iris.

The especial branches destined for the choroid, consisting of both medullated and non-medullated fibres, join within the lamina supra-choroidea to form a wide-meshed plexus, at the nodal points of which larger or smaller groups of ganglion-cells are situated. The plexus so formed contributes numerous fine non-medullated fibres, which proceed to the arteries, accompanying them to their finest ramifications as nervous filaments of increasing delicacy ; ganglion-cells, isolated or in very limited groups, are not infrequently found along the vessels. Since the nervous supply of the choroid is especially distributed to the muscular tissue of the blood-vessels, the component fibres may be regarded as vaso-motor in character.

The *blood-vessels* of the choroid include the branches derived from the short posterior ciliary arteries and the tributaries of the great collecting veins ; the detailed disposition of these vessels has already been considered.

The *lymphatics* of the choroid are represented, according to Alexander,[3] by distinct capillaries which are intimately related to the intercapillary spaces within the chorio-capillaris on the one hand, and to the perivascular sheaths leading to the larger lymph-channels on the other.

THE CILIARY BODY.

Under this name is included the specialized anterior portion of the choroidal tract extending from the ora serrata to the sclero-corneal juncture. The general outline of this region, as seen in meridional sections, is triangular, the outer and longer side lying next the sclero-corneal juncture and the sclera, the short anterior side being bounded by the pectinate ligament, with the included spaces of Fontana and the base of the iris, and the irregular inner border being covered by the deeply pigmented extension of the retinal tunic which rests upon the anterior margin of the vitreous body.

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[1] Sattler: Ueber den feineren Bau der Chorioidea u. s. w., Archiv f. Ophthalmol., Bd. XXII., 1876.

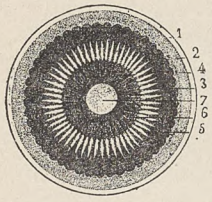
[2] Kerschbaumer: Über Altersveränderungen der Uvea, Archiv f. Ophthalmol., Bd. XXXVIII., 1892.

[3] Alexander: loc. cit.

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The structures included within this area present differences which at once suggest a subdivision of the ciliary body into three secondary portions. The first of these, the *ciliary ring*, appears as a slightly thickened, smooth zone, about four millimetres in width, which extends from the anterior limit of the choroid proper, opposite the ora serrata, as far forward as the base of the irregular projections which mark the inner surface of the adjacent portion of the ciliary body.

Fig. 31.

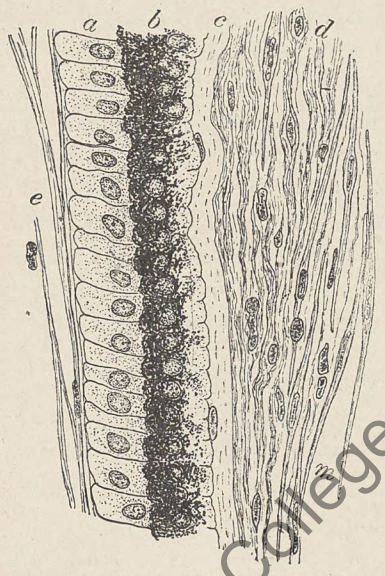


Posterior view of iris and ciliary bodies. (After Sappey.)—1, sclera; 2, choroid; 3, ciliary ring; 4, position of ora serrata; 5, zone of ciliary processes; 6, iris; 7, pupil. Natural size.

The second portion, the *ciliary processes*, includes the anterior part of the inner surface of the body, and is distinguished by the presence of a series of irregular projections or processes which, covered by the pigmented retinal layer, look towards the adjacent vitreous.

The third portion of the ciliary body, in many respects its most important constituent, is formed principally by the fibres of the *ciliary muscle*, a triangular mass of muscular tissue which occupies the outer two-thirds of the ciliary body and provides an essential part of the accommodative apparatus of the eye.

Fig. 32.



Section through the ciliary ring close behind the ciliary processes.—*a*, *b*, the inner and outer layers of the pars ciliaris retinæ; *c*, the continuation of the vitreous membrane; *d*, the continuation of the choroidal connective-tissue stroma containing muscle-cells (*m*) derived from the ciliary muscle; *e*, fibres of attachment of the suspensory ligament of the lens. Magnified 335 diameters.

The *ciliary ring*, or *orbiculus ciliaris*, includes an annular band about four millimetres in width, immediately preceding the anterior limit of the choroid proper as marked by the ora serrata; its inner surface, directed towards the vitreous body, is covered by the pigmented cells of the atrophic layers of the pars ciliaris retinæ, presently to be described.

This portion of the choroidal tract differs in its structure from that of the choroid proper chiefly in the absence of the capillary layer, which ceases at the ora serrata in correspondence with the distribution of the layer of rods and cones of the retina, for whose nutrition the chorio-capillaris is particularly designed. The connective-tissue matrix of the ciliary ring also varies from that of the choroid proper in the greater number of bundles of fibrous tissue, principally meridionally disposed, which it contains. The

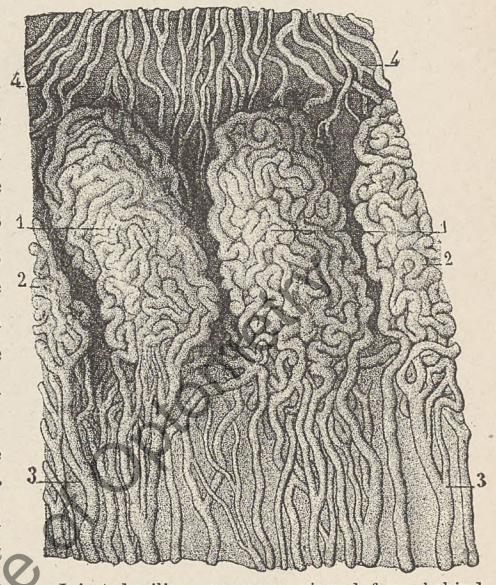
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vitreous membrane is continued over the inner surface of the ciliary ring, but in this location presents numerous thickenings which appear as a reticulation of low ridges; the latter gradually become less conspicuous as they pass towards the ciliary processes, to which they give origin.

While the capillary stratum is no longer present within the ciliary ring, the larger venous trunks are represented by the veins which return the blood from the iris and the ciliary processes as tributaries to the more posteriorly situated venæ vorticosæ. The blood from the greater part of the ciliary muscle, on the other hand, is carried off by vessels emptying into the anterior ciliary veins. The venous channels of this region are provided with adventitious coats and perivascular sheaths.

In addition to the foregoing peculiarities, the stroma of the ciliary ring is in intimate relation with the contractile tissue of the ciliary muscle. As pointed out by Schwalbe,[1] the latter structure must be regarded as a new formation, intercalated between the sclera and the connective-tissue stratum, and contributed by the matrix of the choroidal tract, rather than as an integral part of the latter. The inner surface of the ciliary ring is closely invested, as already noted, by the pigmented layers of the pars ciliaris retinæ, the relation being especially intimate in the recesses between the reticulated ridges on the glassy membrane.

FIG. 33.



Injected ciliary processes viewed from behind. (Sappey.)—1, 2, venous plexuses of tortuous venous radicles composing the bulk of the projections; 3, 3, efferent trunks which become tributaries of the venæ vorticosæ; 4, 4, venous radicles from the iris. Magnified 40 diameters.

The *ciliary processes*, or plicæ ciliares, constitute an annular series of meridionally directed highly vascular folds, about seventy in number, which extend from the anterior limit of the ciliary ring forward and inward to the base of the iris. They are between two and three millimetres in length, .12 to .15 millimetre in breadth, and, at their apices, attain a height of .8 to one millimetre. Seen from the posterior surface (Fig. 31), they constitute a broken ring of radial plications encircling the outer boundary of the iris. Each process begins behind by the apparent fusion of several of the ridges above mentioned as existing on the ciliary ring, and rapidly increases in breadth and height to a point about opposite the

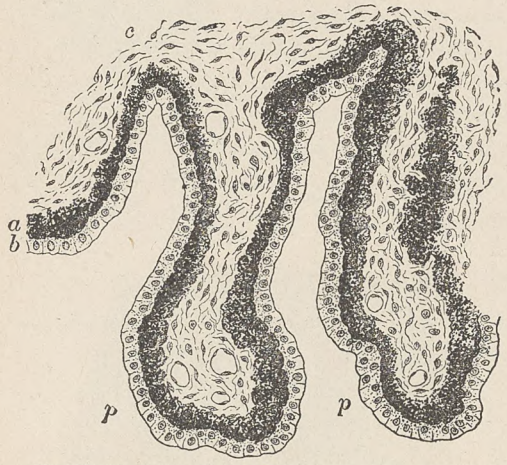
[1] Schwalbe: Anatomie der Sinnesorgane, S. 190, 1887.

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margin of the crystalline lens; the process then abruptly diminishes to the level of the posterior surface of the iris.

Examined in meridional section, each process is represented by a series of irregular projections which vary greatly in size and exact arrangement; they gradually increase in height towards the iris, the maximum elevation being reached in the last projection, which corresponds to the inner angle of the macroscopic structure.

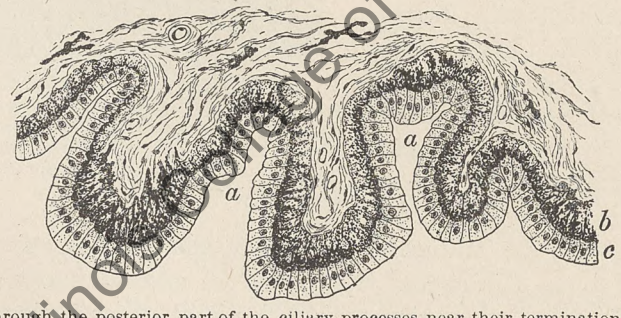
Fig. 34.



Meridional section of the ciliary processes.—*a*, the outer pigmented layer of the pars ciliaris retinæ; *b*, the unpigmented layer of the same; *c*, connective tissue of choroidal tract; *p*, *p*, anterior surface of the processes. Magnified 160 diameters.

The general mass of the ciliary process consists of the thickened stratum of fibro-elastic connective tissue directly continued from the matrix of the ciliary ring. In addition to this tissue, which constitutes the supporting framework of the process, a rich convolution of capillary blood-vessels still further contributes to the bulk of the projections. The inner surface of the ciliary processes is invested by the continuation of the vitreous membrane, which here is somewhat thickened, attaining a thickness of from .003 to .004 millimetre, and separates the connective-tissue stratum from the pigmented covering derived from the atrophic pars ciliaris retinæ.

Fig. 35.



Section through the posterior part of the ciliary processes near their termination.—*a*, *a*, narrow, gland-like recesses lined by *c*, *b*, the inner and outer layers of the pars ciliaris retinæ. Magnified 155 diameters.

The arteries distributed to the ciliary processes proceed from the greater circulus arteriosus, situated at the periphery of the iris, to the anterior end of the plications, the usual arrangement, according to Leber, being such

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that the smaller arterioles supply each a single process, while the larger branches suffice for several folds.[1] After attaining the anterior end of the process, the arteriole breaks up into numerous capillary vessels, the tor-

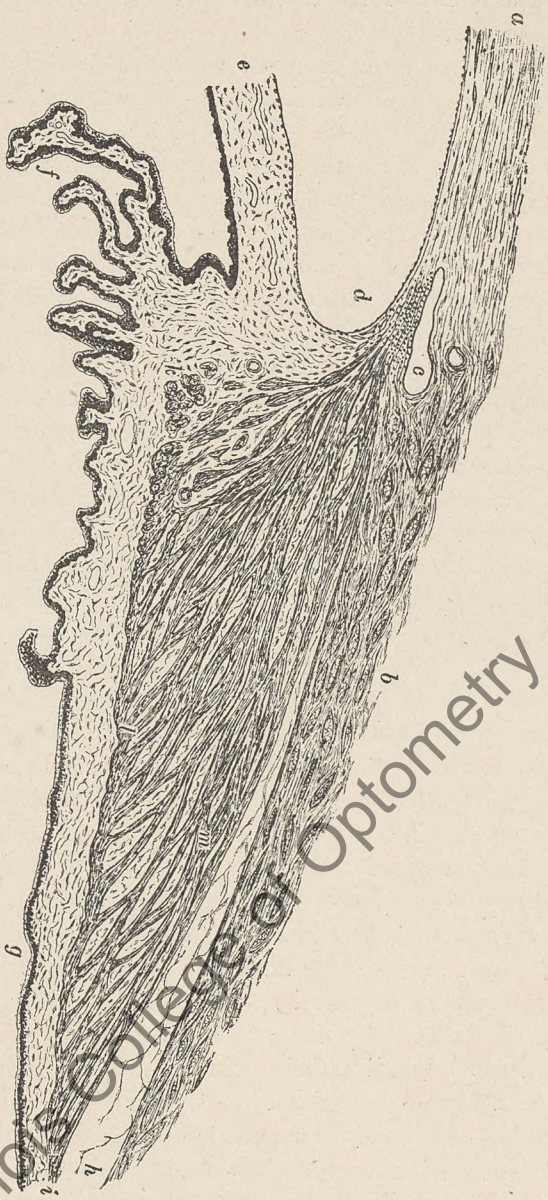


FIG. 36.

Meridional section of the ciliary region.—*a*, cornea; *b*, sclera; *c*, canal of Schlemm; *d*, angle of anterior chamber; *e*, iris; *f*, ciliary processes; *g*, ciliary ring; *h*, artificially expanded supra-choroidal space; *i*, posterior termination of the ciliary muscle; *m*, meridionally disposed fibres of the latter; *l*, inner termination of radial fibres; *k*, circularly disposed fibres of Müller's ring muscle. Magnified 40 diameters.

tuous courses of which produce the elaborate convolutions so conspicuous in injected preparations of these structures.

The capillary net-works gradually pass over into the mesh-work of

[1] Leber: Die Circulations- und Ernährungsverhältnisse des Auges, Graefe u. Saemisch's Handbuch, Bd. II., 1876.

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venous radicles, which converge to form several minute veins for each process; the latter, in turn, emerge at the posterior extremity of the fold, and, after a meridional and posterior course across the ciliary ring towards the great venous foci of the vascular tunic, finally become tributaries of the large venæ vorticosæ.

The *ciliary muscle* forms the most conspicuous constituent of the ciliary body, appearing in meridional sections as a triangular field of involuntary muscular and connective tissue. This area is bounded by the sclerotic coat externally, extending from the sclero-corneal juncture anteriorly as far as the ciliary ring posteriorly, and is limited on its internal and posterior surfaces respectively by the pectinate ligament and the connective-tissue stratum contributed by the choroidal tract. The ciliary muscle in its entirety forms a prismatic annular band which encircles the angle of the anterior chamber and the root of the iris.

When critically examined, the triangular area of cross-sections of the muscle is seen to be composed, in addition to the connective tissue, of interlacing branches of involuntary muscle which are disposed in three principal directions,—meridionally, radially, and circularly.

The meridionally disposed muscular bundles are closely grouped and separated by small bands of interfascicular connective tissue, thus forming a compact outer layer next the sclera, the *tensor choroideæ*, to which the trabeculæ of the supra-choroidal space are attached. The meridional fibres take origin especially from the scleral process and the reticular tissue constituting the inner wall of Schlemm's canal; posteriorly, they fade away into the tissue of the choroidal tract, to which they are attached or inserted by means of delicate tapering and often interlacing processes. The fibres situated most externally pursue a typically meridional course, the tendency to assume a radial direction becoming more and more pronounced as the inner and posterior limits of the muscle are approached.

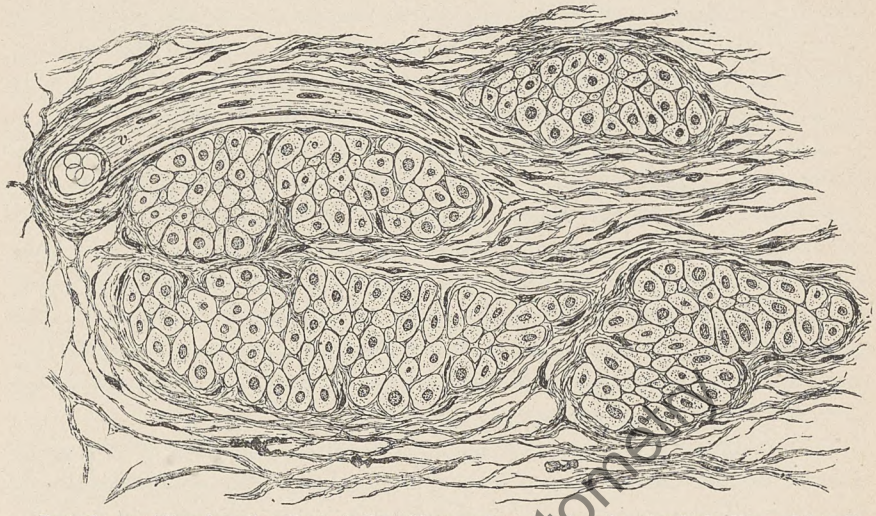
The radially arranged fibres are, therefore, not sharply defined from the meridional bundles, since the change in disposition is very gradually effected, the two sets of fibres blending towards the periphery. The radial bundles are much more loosely arranged, and form a reticulation in which the muscular bands are separated by considerable tracts of connective tissue. Anteriorly, the radial fibres are attached somewhat farther forward than are the meridional bundles, their point of origin being the tissue of the inner wall of Schlemm's canal and the trabeculæ derived from the peripheral splitting up of the membrane of Descemet. Beginning at their point of origin, the interlacing muscular bundles diverge posteriorly and internally in a fan-like manner, the innermost bundles passing towards the ciliary processes, the more externally situated reaching to and beyond the anterior limits of the ciliary ring. The posterior border of the muscular reticulum formed by the radial fibres is irregular in outline, and occupied at the extreme boundary by muscle bundles which bend sharply to assume a circular course.

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The circularly disposed fibres, in addition to those just noted, are collected principally at one point, where they form an annular group which occupies the inner posterior angle of the general muscular triangle formed by the ciliary muscle, and surrounds the base of the iris. These bundles constitute the *circular* or *ring muscle of Müller*, as contrasted with the *tensor choroideæ*, composed of the remaining meridional and radial portions of the ciliary muscle.

In emmetropic eyes the general mass of the ciliary muscle approaches in outline a right-angled triangle, the greatly elongated hypothenuse of which is represented by the scleral border, the other sides being the short

FIG. 37.



Part of a meridional section through the ciliary region, showing the circularly disposed bundles composing Müller's muscle in transverse section.—*v*, small vein within the connective-tissue stroma. Magnified 335 diameters.

iridial and long choroidal surfaces. The apex of the angle is somewhat rounded by the circular fibres of Müller. Pronounced hypermetropic and myopic eyes often exhibit marked variations from the normal form of the muscle, as described by Iwanoff and confirmed by later investigations. These changes depend largely upon the over- or under-development of the circular fibres. In myopia, Müller's bundles are more or less atrophic, the angle of the ciliary muscle consequently appearing relatively obtuse. In hypermetropia, on the contrary, the excessive demands made upon these fibres result in their unusual development, with corresponding preponderance of this portion of the mass, in consequence of which the angle becomes acute, the including sides subtending less than the approximate ninety degrees of the normal muscle.

The ciliary processes, in addition to affording support and partial attachment to the suspensory apparatus of the crystalline lens, are undoubtedly closely concerned in the production of the aqueous humor which occupies both the anterior and the posterior chamber.

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Deutschmann [1] convincingly demonstrated the active rôle played by this portion of the uveal tract in the secretion of the aqueous humor by excising the ciliary body and noting the subsequent arrest of secretion of this fluid. The later experiments and observations of Schoeler,[2] Leplat,[3] Gifford,[4] Knies,[5] and Greeff[6] all emphasize the important relations between the ciliary processes and the secretion of the aqueous humor, as well as establish the existence of the current of this fluid from the posterior chamber through the pupil into the anterior chamber.

While it may be regarded as established that the aqueous humor is produced through the agency of the ciliary processes, the determination of the structures especially engaged in this secretion has been less exact. The most definite conclusions concerning this point are those advanced by Collins,[7] who, under the name of "ciliary glands," describes epithelial extensions of the outer layer of the pars ciliaris retinæ, which he regards as the structures engaged in the elaboration of the aqueous fluid.

The ciliary zone of the rudimentary anterior segment of the inner tunic of the eyeball, including the portion of the tract extending from the ora serrata to the root of the iris, consists, as does, indeed, the entire tract, which reaches as far as the anterior pupillary margin, of two layers of cells. These strata, which represent the inner and outer lamellæ of the secondary optic vesicle, differ in their histological details. While a fuller account of these structures will be found in connection with the description of the nervous tunic, a few facts regarding the constitution of the pars ciliaris retinæ must here be anticipated for the present purpose.

The rudimentary retinal expansion which covers the inner surface of the ciliary ring and the ciliary processes consists of a double layer of epithelial elements. The inner of these is composed of cells possessing a well-pronounced columnar form; the outer, of elements which are lower and assume often a more cuboidal character. Over the posterior surface of the iris, as well as over the anterior and most conspicuous parts of the ciliary processes, the inner cells are loaded with dark pigment; towards the posterior and less projecting parts of the processes this pigment becomes much less intense,

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[1] Deutschmann: Ueber die Quellen des Humor aqueus im Auge, Archiv f. Ophthal., Bd. XXVI., 1880.

[2] Schoeler: Ueber das Fluorescein in seiner Bedeutung für Erforschung des Flüssigkeitswechsels im Auge, Archiv f. Anat. u. Physiolog., Physiolog. Abth., 1882.

[3] Leplat: Études sur la nutrition du corps vitré, Annales d'Oculistique, t. XCVIII., 1887.

[4] Gifford: Weitere Versuche über die Lymphströme und Lymphwege des Auges, Archiv f. Augenheilkunde, Bd. XXVI., 1893.

[5] Knies: Ueber die vorderen Abflusswege des Auges und die künstliche Erzeugung von Glaukom, Archiv f. Augenheilkunde, Bd. XXVIII., 1894.

[6] Greeff: Neue Befunde zur Kenntniss des Flüssigkeitswechsels im Auge und zur Lehre von der Fibrinbildung im Kammerwasser, Bericht über d. 23. Versamml. d. Ophthalmol. Gesellsch. zu Heidelberg, 1893.

[7] Collins: The Glands of the Ciliary Body in the Human Eye, Trans. of the Ophthal. Society of the United Kingdom, vol. XI., 1891.

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and is limited to the outer portions of the cells; while over the ciliary ring the elements composing the inner layer are almost, if not entirely, devoid of colored particles. There is thus a progressive decrease of the pigment within the cells of the inner lamella from the bases towards the apices of the ciliary processes. The outer layer, on the contrary, remains more or less deeply pigmented throughout its extent, and over the ciliary ring and the apices of the processes the cells contain a considerable amount of colored particles.

When carefully examined in meridional sections, the outer contours of the elements of the external layer appear irregular, and here and there the adjacent tissue is encroached upon by minute cylindrical projections. These latter structures, upon examination after removal of the obscuring pigment by bleaching, Collins describes as composed of aggregations of epithelial cells arranged after the manner of the elements composing tubular glands in other situations, which he regards as true secreting tissue composing the glands of the ciliary body. These cylindrical projections from the outer cell-stratum are most frequent and conspicuous in the plicated portion of the ciliary region, being particularly numerous and developed at the junction of the apices of the ciliary processes and the smooth ciliary ring. Collins regards these minute outgrowths as the glandular apparatus by means of which the aqueous humor is secreted. Additional weight in support of this view is found, according to this author, in the greatly exaggerated and hypertrophied condition of these "glands" in pathological processes associated with excessive secretion of the aqueous humor, as in serous iritis. Sections of the ciliary region of eyes so affected display the presence of conspicuous tubular proliferations closely associated with the covering of this part of the uveal tract.

That the ciliary processes, at least in part, if not as a whole, are intimately and directly related to the production of the aqueous humor is established beyond dispute; critical study of the foregoing structures described as the ciliary glands, however, will fail to convince many, and among them is Leber,[1] that these minute cylindrical projections, which are separated from the posterior chamber by means of the unbroken inner layer of tall columnar cells of the pars ciliaris retinæ, suffice for the elaboration of the no inconsiderable quantity of fluid continually escaping from the eye. The broader view of Nicati,[2] who attributes the secretion of the humor aqueus to the "uveal gland," the epithelium of which is represented by the pars ciliaris retinæ, the blood-supply by the rich vascular distribution within the adjacent structures, and the contractile tissue by the cilio-choroidal muscle, offers a more comprehensive interpretation.

The Blood-Vessels of the Ciliary Body.—The blood-vessels especially supplying the ciliary muscle are derived from two sources,—from the long

[1] Leber: Ergebnisse der Anatomie u. Entwickelungsges., Bd. iv., 1894, p. 175.

[2] Nicati: La glandula de l'humeur aqueuse, Compt.-rend. hebd. de la Soc. de Biolog., Sér. 9, t. III., 1892.

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and the anterior ciliary arteries. These vessels, in their course through the anterior part of the muscle to gain the root of the iris, where they form the larger arterial circle, give off branches which anastomose with considerable frequency and constitute a somewhat incomplete arterial circuit, the *circulus arteriosus musculi ciliaris;* from the latter minute twigs pass in various directions into the substance of the muscle for the supply of the muscular tissue.

The arteries supplying the ciliary processes are derived from the *circulus iridis major*, as branches which pass backward, traversing the inner part of the ciliary muscle, to reach the anterior extremities of the plications. On

FIG. 38.

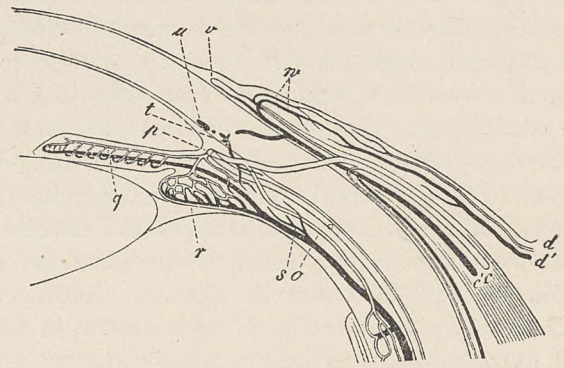


Diagram of vascular supply of anterior segment of eye. (Leber.)—*c*, *c'*, anterior ciliary artery and vein; *d*, *d'*, posterior conjunctival vessels; *o*, recurrent twig to choroid; *p*, circulus arteriosus iridis major in section; *q*, vessels of iris; *r*, vessels of ciliary processes; *s*, vein returning blood from iris and ciliary process; *t*, tributary of anterior ciliary vein from ciliary muscle; *u*, circulus venosus (canal of Schlemm); *v*, vascular loops of corneal limbus; *w*, anterior conjunctival vessels.

entering the latter—a single artery often providing for more than one process—the main stem rapidly breaks up into secondary branches, which soon pass over into the intricate convolutions forming so large a part of the entire fold.

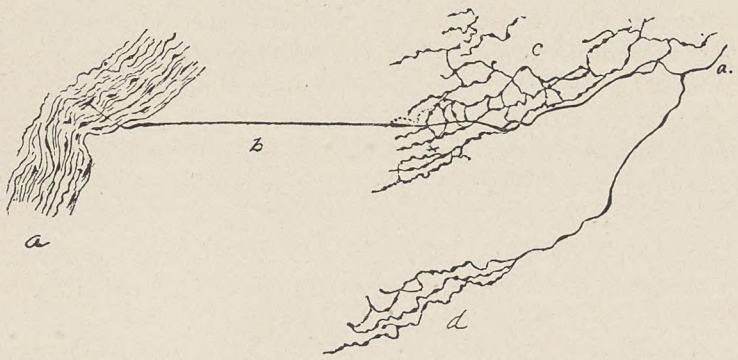
The venous radicles draining the ciliary muscle become tributary to two distinct groups, the anteriorly and the equatorially situated veins. A portion of the blood is carried inward and backward to join that carried by the veins returning the blood from the ciliary processes; it is, therefore, finally taken up and conveyed from the deeper structures by the great equatorial trunks, the venæ vorticosæ; another portion of the blood from the ciliary muscle is conducted forward and outward by means of vessels which pierce obliquely the sclerotic coat and empty into the anterior ciliary veins. During their passage through the fibrous tunic they come into proximity to the canal of Schlemm and receive the small tributaries proceeding from that channel, by means of which, as already noted, indirect communication is established between the annular sinus and the anterior ciliary veins.

The Nerves of the Ciliary Body.—The remarkable functional activity of the structures included within the ciliary body leads to the anticipation of the existence of a rich nervous supply to this region.

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The anterior ramifications of the long ciliary nerves, together with filaments contributed by the short ciliary trunks, on entering the ciliary body unite to form an annular plexus, the *orbiculus gangliosus*, within the substance of the ciliary muscle. The varied character of the component fibres of these branches explains the presence of motor, sympathetic, and sensory nerve-fibres within this plexus.

FIG. 39.



Nerve-terminations within the ciliary muscle. Methylene-blue staining.—*a*, bundle of medullated nerve-fibres giving off a lateral twig (*b*). which divides into branches which break up into the terminal arborizations (*c*, *d*). (After Agababow.)

The more recent investigations of Agababow and Arnstein[1] have added to our definite knowledge concerning the complex disposition of the nerves of this region. According to these observers, four sets of nerve-fibres may be demonstrated within the ciliary body of the cat, and, with modifications, also within that of man. These groups of nervous filaments comprise: 1, the vaso-motor fibres supplying the vascular tissues; 2, the motor fibres ending within the tissue of the ciliary muscle; 3, the sensory fibres, forming a subscleral distribution; 4, fibres terminating in ramifications within the intermuscular tissue of the ciliary muscle.

The *vaso-motor fibres* are especially concerned in the innervation of the walls of the blood-vessels, within the outer parts of which they break up into fibrillæ which penetrate the muscular tunic. The distribution of the vaso-motor fibres to the ciliary processes has been carefully studied by Meyer[2] and Grünhagen.[3]

The *motor fibres*, destined particularly for the tissue of the ciliary muscle, possess a characteristic arrangement, in which the finer fibrillæ pursue a course largely corresponding with the disposition of the muscle elements. The slender straightly running fibrillæ present minute varicosities, and terminate in free endings of great delicacy between the contractile cells.

The *sensory fibres* of the ciliary body, which in the cat and some other

[1] Agababow und Arnstein: Die Innervation des Ciliarkörpers, Anatom. Anzeiger, Bd. VIII., No. 17, 1893.

[2] Meyer: Die Nervenendigungen in der Iris, Archiv f. mik. Anat., Bd. XVII., 1880.

[3] Grünhagen: Die Nerven der Ciliarfortsätze des Kaninchens, Archiv f. mik. Anat., Bd. XXII., 1883.

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animals are represented by a superficial plexus occupying the outer subscleral layers, in man are connected with special expansions or "reticulum-plates." Critical examination of these structures with high powers shows them to be composed of fibrillæ of the greatest tenuity.

Additional sensory fibres, constituting the foregoing fourth group, bear an intimate relation to the ciliary muscle. The twigs given off from the annular plexus consist principally of medullated fibres; they soon divide and intertwine, and contain sparingly interspersed ganglion-cells, chiefly along the course of the thinner nerve-bundles. On following the medullated fibres in their further ramifications within the mass of the ciliary muscle, they are seen to give off small offshoots, which retain their medullary sheath until they have reached a different plane, when they soon divide into two non-medullated fibres. The latter almost immediately break up into a number of secondary fibrillæ, which in turn are resolved into terminal threads, the entire group of fibrillæ forming a special end-arborization, of which two or more are connected with the filaments derived from a single primary lateral twig.

The terminal arborizations connected with the nerves in question are distinguished from other nervous endings within the ciliary muscle by the relatively great thickness of the varicose fibrillæ, which end in free knob-like expansions. These end-arborizations are situated at various levels, but occupy particularly the posterior and inner segment of the ciliary body. They lie within the intermuscular connective tissue between the bundles composing the ciliary muscle. According to Arnstein,[1] these terminal ramifications represent a special nervous apparatus for the perception of muscle-sensibility excited mechanically by the contraction of the surrounding muscular bundles.

THE IRIS.

The iris constitutes the anterior and inner segment of the vascular tunic of the eyeball, forming the perforated membrane or diaphragm which stretches across in front of the crystalline lens. Its inner or pupillary margin rests upon the anterior surface of the lens; its periphery or root is connected with the choroidal tract just anterior to the ciliary processes.

Viewed in section, the iris presents, in addition to its variously tinted stroma, covered in front by the endothelium of the anterior chamber, a deeply pigmented posterior stratum directly continuous with the pigment layers clothing the ciliary processes; this dark lamella represents the rudimentary anterior segment of the nervous tunic, and constitutes the *pars iridica retinæ*. The iris, therefore, is composed of two genetically distinct parts,—that contributed by the mesoderm, and that secondarily derived from the ectoderm through the optic vesicle.

The various components of the iris and their morphological relations may be grouped as follows:

[1] Arnstein: loc. cit., p. 560.

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1. *Anterior endothelium.*
2. *Anterior boundary layer.*
3. *Vascular stroma layer.*
4. *Posterior limiting lamella.*

} Continuation of the mesodermic tissues of the choroidal tract, constituting the *stroma zone.*

5. *Pigment layer.* { *a.* Anterior layer of *pigmented spindle-cells*, representing OUTER LAYER
b. Posterior layer of *pigmented polygonal cells*, representing INNER LAYER } of optic vesicle.

The *anterior endothelium* consists of a single layer of irregular polyhedral plates, composed of finely granular protoplasm and containing ovoid or reniform nuclei, which are uninterruptedly continued over the front surface of the iris as far as the pupillary margin. This endothelium, the

FIG. 40.



Radial section of iris.—*a*, endothelium; *b*, anterior boundary layer; *c*, vascular stroma; *e*, posterior limiting lamella; *f*, pigmented retinal zone; *v*, blood-vessels. Magnified 170 diameters.

presence of which is demonstrable after silver staining, is a part of the general lining of the anterior chamber; it is, therefore, a direct continuation of the endothelial cells which cover the membrane of Descemet and invest the trabeculæ of the ligamentum pectinatum. Even when the stroma layer is loaded with pigment, as in irides of very deep color, the cells of the anterior endothelium remain clear and uninvaded by pigment.

The *anterior boundary layer* has no existence as an independent layer, since it consists of the modified and condensed foremost stratum of the stroma, in which the connective-tissue cells of the general iris-stroma are unusually closely arranged on account of the relatively small amount of the

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intercellular fibrous tissue and small size of the interfascicular lymph-spaces. As a result of these peculiarities the cells lie nearer together, producing an appearance which Michel[1] interprets as indicating a layer of reticulated tissue somewhat resembling a dense lymphoid structure. The layer under consideration, however, differs from ordinary iridial stroma, as pointed out by Koganeï,[2] only in being more condensed, the existence of a reticulum seemingly composed almost exclusively of irregularly spindle and stellate plate-like elements, as assumed by Michel, being suggested by the inconspicuous representation of the fibrous bundles in this part of the iris. The fibrous tissue is, however, distinctly present, and exists, as emphasized by Retzius,[3] in the form of irregularly interlacing, extremely delicate bundles, which pass between the cells as far as the anterior endothelium. The irregular connective-tissue cells occupying the anterior layer, which are sometimes round, oval, or stellate elements, in the deepest part of the boundary layer assume the disposition of the elements of the general iris-stroma, into which they insensibly pass.

The minute clefts which occupy the interspaces between the elements constituting the anterior boundary layer represent lymph-spaces, and sometimes contain lymph-corpuscles or migratory cells in varying number, as in other parts of the iris-stroma. At the posterior margin of the boundary layer the intercellular clefts become of larger size, and gradually pass into the lymph-spaces of the stroma layer. In deeply colored irides the protoplasm of the cells composing the anterior boundary layer, as well as their processes, becomes invaded by pigment particles. Blood-vessels are wanting within this part of the iris.

The *vascular stroma layer*, which constitutes the bulk of the iris, consists of a loosely disposed mesh-work of connective-tissue fibres and cells supporting a rich supply of blood-vessels and nerves and enclosing irregular lymph-spaces. In addition to these elements, this stratum, in the vicinity of the pupillary margin, contains the muscular tissue constituting the *sphincter pupillæ*, as well as an irregular layer of radially disposed muscle-bundles which extend from the pupillary towards the marginal zone, and represent an imperfect *dilator pupillæ*.

The strength of the supporting framework depends less on the connective-tissue elements than upon the radially coursing blood-vessels and nerve-trunks which they invest (Schwalbe), and around which they form sheaths of considerable size. The structural elements composing the layer of vascular stroma include delicate bundles of fibrous tissue, on and between which lie the irregular connective-tissue cells. While the fibrous tissue is aggregated principally as the sheaths investing the vessels and the nerves,

[1] Michel: Die histologische Structur des Irisstroma, Erlangen, 1875.

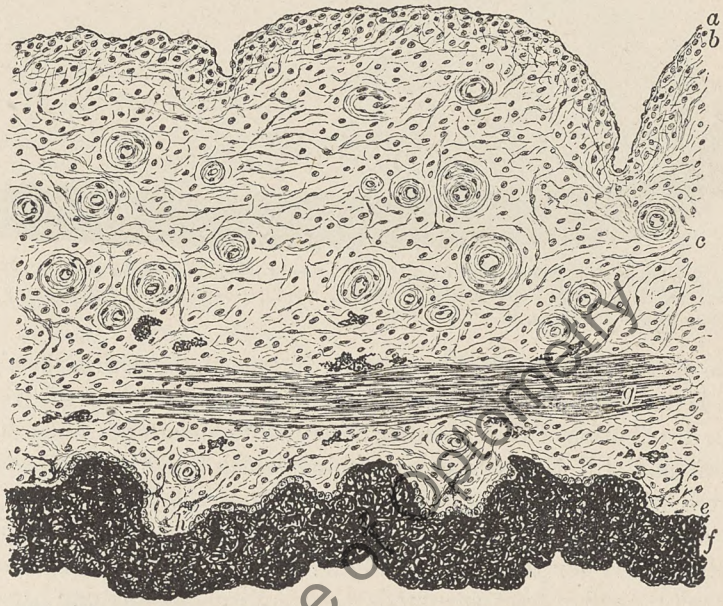
[2] Koganeï: Untersuchungen über den Bau der Iris des Menschen und der Wirbelthiere, Archiv f. mik. Anat., Bd. xxv., 1885.

[3] Retzius: Zur Kenntniss vom Bau der Iris, Biologische Untersuchungen, Neue Folge, v., 1893.

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the intervening territory is occupied by delicate bands irregularly interwoven to form a loose or spongy tissue, the interfibrillar interstices of which may be regarded as lymph-spaces. The connective-tissue cells are particularly numerous in the vicinity of the larger perivascular sheaths, accompanying the blood-vessels in conspicuous groups; within the general loose mesh-work characterizing other parts of the stroma layer the cells are much less numerous. The fibrous investments of the blood-vessels, arteries as well as veins, are particularly conspicuous in sections passing parallel to the pupillary margin, in which the radially disposed vessels are cut generally at right angles. These perivascular sheaths, which in thickness not infrequently equal the external diameter of the enclosed vessel, are composed principally of circularly disposed fibres; the latter often deviate sufficiently

FIG. 41.



Tangential section of iris.—*a*, endothelium; *b*, anterior boundary layer; *c*, vascular stroma; *e*, posterior limiting lamella; *f*, pigmented retinal zone; *g*, portion of sphincter pupillæ muscle cut parallel to course of fibres; *h*, transversely cut dilator fibres. Magnified 170 diameters.

in their transverse arrangement to produce obliquity, which results in an interweaving of the fibrillæ. While the circular fibres constitute the most important part of the sheath, Retzius[1] has shown that longitudinal fibrillæ exist both without and within the chief fibrous layer, the perivascular investment thereby materially gaining in strength. A perivascular lymph-space usually separates the sheath from the blood-vessel, the exterior of the latter being invested by a more or less perfect endothelial covering.

The stroma in dark irides contains a variable amount of pigment, distributed principally as irregular aggregations of pigmented cells in which

[1] Retzius: loc. cit.

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the nuclei alone remain uninvaded; here and there additional smaller non-nucleated masses of colored particles are encountered. The anterior layer and the pupillary zone are the portions of the iris-stroma that contain the pigment-cells in greatest number; in irides of only moderate darkness these situations include almost the entire pigment. The stroma of very dark irides presents a much more general distribution of the pigment, since in these cases all portions of the stroma layer are filled with the colored particles; the latter are contained either within irregular spherical masses of pigment-cells or within more isolated stellate elements. The vicinity of the circulus arteriosus minor—that is, the outer margin of the pupillary zone—is especially rich in accumulations of pigment.

FIG. 42.



Radial section of pupillary zone of iris.—*a*, termination of pigmented layers at pupillary margin; *b*, stroma layer; *c*, transversely cut bundles of sphincter pupillæ; *d*, pigmented retinal zone; *e*, dilator fibres. Magnified 70 diameters.

The *muscular tissue* which, as already intimated, lies within the vascular stroma layer forms one of the most important constituents of the iris.

The distribution of this muscular tissue, while a matter of much interest, has been and still is a subject concerning which the views of competent observers widely diverge. While the details of the arrangement of the iridial musculature, particularly the presence or absence of a dilator pupillæ, are still matters for discussion, it is agreed that anatomically the most important muscular tract surrounds the pupil as an annular band,—the *sphincter pupillæ*.

The latter consists of a zone of involuntary muscle, varying between .040 and .080 millimetre in width, according to the state of contraction, and measuring about one-tenth as much in thickness; it is situated nearer the posterior than the anterior surface of the iris-stroma. The individual muscle-bundles composing the pupillary sphincter somewhat interlace during their circular course, being contained within and separated from one another by delicate investments of connective tissue.

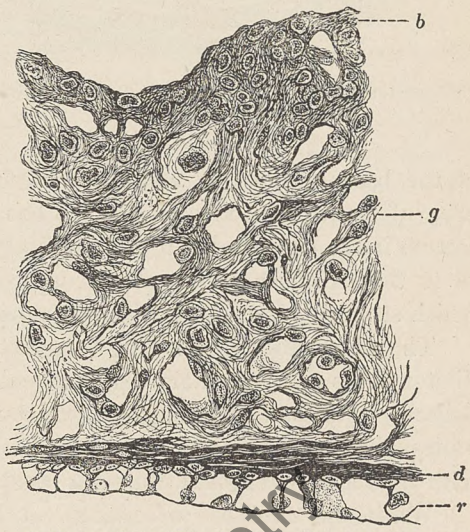
The muscle extends almost, but not quite, to the pupillary margin, the immediate free border of the latter being composed of the attenuated continuation of the retinal layers, which thus shut out the iris-stroma from the pupil. During contraction, however, the pigmented retinal layers become compressed to such a degree that the sphincter muscle apparently forms the

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direct boundary of the pupillary opening. The observation of Steinach,[1] that the muscular elements of the sphincter are sometimes pigmented, is of interest in connection with the presence of colored particles within the spindle-cells of the posterior boundary layer of the iris.

In marked contrast to our definite knowledge regarding the universally admitted presence of a sphincter muscle stand the data concerning the existence of an antagonizing dilator pupillæ. Notwithstanding, however, the disagreement as to their interpretation, the presence of certain anatomical details has been established by many observations.

FIG. 43.



Radial section of iris of rabbit. (Retzius.)—*b*, anterior boundary layer; *g*, vascular stroma layer; *d*, dilator fibres; *r*, retinal layer. Magnified about 300 diameters.

It is admitted by all that the iris-stroma is separated from the deeply pigmented posterior zone by a delicate stratum, the posterior boundary layer, or membrane of Bruch, within which, or at least closely associated with it, exist numerous radially disposed delicate spindle fibre-cells. These elements, often more or less pigmented, are the particular objects concerning which investigators disagree, since some regard the spindle-cells as muscular in nature, while others consider them as modified connective tissue.

The character of these cells has been repeatedly the subject of critical investigations by competent observers in the iris of the albino rabbit, which tissue, owing to the absence of the obscuring pigment, offers an unusually favorable opportunity of study.

Sections of such tissue, either when cut meridionally or parallel to the surface of the iris, demonstrate the presence of long, delicate spindle-cells, the general form and nuclei of which strongly resemble elongated muscular elements. These cells are especially well displayed in tissues fixed in a four per cent. solution of formaldehyde and stained with hæmatoxylin. The spindle-cells in the rabbit, however, do not constitute a continuous layer, but are disposed as delicate bundles radiating from the pupillary margin well towards the ciliary zone. The presence of similarly arranged spindle-cells

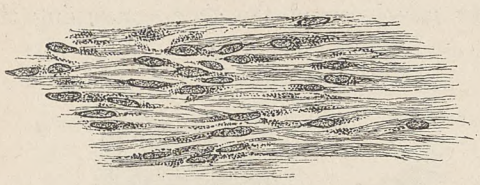
[1] Steinach: Über den Sphincter Pupillæ des Frosches, Archiv f. d. ges. Physiologie, Bd. LIII., 1893.

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has been established by Heese[1] in a number of other animals, including the cat, dog, sheep, ox, and pig.

Direct observations confirming the existence of corresponding elements within the human iris have been made by a number of investigators, among which the testimony of Merkel,[2] Retzius,[3] and Schäfer[4] is the most positive. The last-named observer states, "I have myself obtained unmistakable evidence of the presence of a thin layer of fibres at the back of the iris, under the pigment-cells, having all the appearance of flat, plain muscle-cells." The study of numerous sections of human irides cut parallel to the pupillary margin leads the writer to agree as to the existence of an almost unbroken layer of elongated elements which strongly resemble involuntary muscle-cells.

Fig. 44.



Surface view of dilator fibres of human iris. (Retzius.) Magnified about 400 diameters.

The observations of Ewing[5] suggest the close relations between the dilator fibres and the ciliary region: he describes the presence of numerous delicate bundles of radiating connective-tissue fibres, which pass from the valleys between the ciliary processes, through the root of the iris, to join with the radially disposed muscular bundles representing the dilator.

While the existence of a more or less complete stratum of delicate spindle-cells within the posterior border of the stroma layer of the iris of man and many other animals may thus be assumed as positively demonstrated, the interpretations as to the exact nature of these elements are far from identical. The difficulty of determining the nature of the cells in question solely upon their morphological characteristics is admitted by those most skilled in microscopical investigations, and even so experienced an observer as Retzius confesses his inability to decide positively the muscular character of the spindle-cells from their histological details.

The authorities, however, who have regarded the evidence as sufficiently conclusive to warrant the belief in the existence of a definite dilator pupillæ muscle include a number of the most trustworthy observers, among whom are Henle, Kölliker, Luschka, Merkel, Dogiel, Eversbusch, Schäfer, and others. Conspicuous among those who, on the other hand, consider

[1] Heese: Ueber den Einfluss des Sympathicus auf das Auge, insbesondere auf die Irisbewegung, Archiv f. d. ges. Physiolog., Bd. LII., 1893.

[2] Merkel: Ergebnisse der Anatomie u. Entwickelungsges., Bd. III., 1893 (Anmerkung, S. 288).

[3] Retzius: Zur Kenntniss vom Bau der Iris, Biologische Untersuch., Neue Folge, v., 1893.

[4] Schäfer: in Quain's Anatomy, 10th ed., vol. III., Pt. 3, 1894.

[5] Ewing: Ueber ein Bauverhältniss des Iris-Umfanges beim Menschen, Archiv f. Ophthalmol., Bd. XXXIV., 1888.

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the muscular nature of the spindle-cells as insufficiently established, and therefore look upon these elements as elastic in character, are Schwalbe and Grünhagen. The latter, who has long regarded the expansive movements of the iris as associated with the contraction of the blood-vessels, has admitted in a more recent paper[1] that the finely fibrillar ground-substance of Bruch's membrane possesses muscular contractility: Grünhagen's views, therefore, are in closer accord with those of the majority of observers than formerly. As a result of his comparative and embryological investigations, Gabrielides[2] also accepts and figures a dilator in the human iris.

In connection with the question of the presence of a dilator muscle in man, the fact is suggestive that a distinct dilator pupillæ exists not only in birds, where a robust dilator is found, but also in many mammals, as established by the comparative investigations of Koganeï[3] and of Dostoiewsky.[4] Within the iris of the seal and the common otter the dilator is very well developed and constitutes a conspicuous structure; that of the otter, according to Eversbusch,[5] in correspondence with the triangular form of the pupil, consists of three bands of radially disposed fibres.

The admitted uncertainty of definitely establishing the muscular character of the spindle-cells upon purely histological data has given great value to physiological investigations concerning the movements of the iris, as capable of supplying additional corroborative evidence in connection with the existence of a pupillary dilator muscle. The various views held by observers who from time to time have offered explanations concerning the phenomena attending the movements of the iris may be arranged, as suggested by Heese,[6] under three general groups.

1. A sphincter and a dilator muscle both exist; the former is controlled by the oculo-motor nerve, the latter is innervated by the sympathetic. The movements of the iris and its conditions of dilation or contraction are, therefore, the direct result of the antagonizing influence of these two muscles.

2. A dilator muscle does not exist, the size of the pupil being regulated by the balance between the contraction of the sphincter and the elasticity of the iris-stroma. The influence of the sympathetic upon the pupil is secondary, being directly exerted upon the blood-vessels, which by their

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[1] Grünhagen: Ueber die Mechanik der Irisbewegung, Nachtrag, Archiv f. d. ges. Physiologie, Bd. LIII., 1893.

[2] Gabrielides: Recherches sur l'embryogénie et l'anatomie comparée de l'angle de la chambre antérieure chez le poulet et chez l'homme, Archiv. d'Ophthal., t. XV., 1895.

[3] Koganeï: Untersuch. über den Bau der Iris des Menschen und der Wirbelthiere, Archiv f. mik. Anat., Bd. XXV., 1885.

[4] Dostoiewsky: Ueber den Bau des Corpus ciliare und der Iris von Säugethieren, Archiv f. mik. Anat., Bd. XXVIII., 1886.

[5] Eversbusch: Vergleichende Studien über den fein. Bau der Iris der Säugethieren, Zeitsch. f. vergl. Augenheilkunde, Bd. III., 1885.

[6] Heese: Ueber den Einfluss des Sympatheticus auf das Auge, insbesondere auf die Irisbewegung, Archiv f. d. ges. Physiolog., Bd. LII., 1893.

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thereby induced contraction effect a mechanical dilation of the pupillary opening.

3. A dilator muscle does not exist, but the dilation of the pupil following stimulation of the sympathetic nerve is due, not to the contraction of the blood-vessels, but to a restraining or inhibitory action exerted by the sympathetic upon the sphincter. In consequence of such influence brought about by the sympathetic nerve, the dilation follows as the result of the temporary inaction and partial passiveness of the sphincter muscle.

The physiological aspects of the pupillary movements have been exhaustively considered in an elaborate paper by Langley and Anderson,[1] to which the reader is referred for a critical discussion of the various views pertaining to the changes within the iris, as well as for the details of the interesting experimental investigations there recorded. The present purpose will be served by a brief account of the conclusions arrived at by these authors.

The experimental proofs of the existence of a radially arranged contractile substance within the iris adduced by Langley and Anderson include the demonstration of the following facts:

1. When local dilation of the pupil passes a certain limit, the opposite side of the iris is dragged towards the stimulated side; that this displacement is not due to inhibition of the sphincter muscle is shown by the fact that the sphincter can be made to contract at the same time.

2. If a radial strip of iris be isolated from the adjacent parts of the iris, stimulation of the sympathetic causes shortening of the thus isolated strip. This shortening may be produced prior to and without any contraction of the blood-vessels.

3. Direct examination of the iris during stimulation of the cervical sympathetic shows that dilation of the pupil precedes the contraction of the vessels. The dilating action of the sympathetic is thus demonstrated to be independent of contraction of the blood-vessels.

4. There is no proof of elastic tissue in the iris, since a radial strip does not always retract on being stretched; if the iris be left until its muscular tissue is dead, a radial strip does not shorten.

5. There is no evidence that the sympathetic causes inhibition of the sphincter; it causes, on the contrary, radial shortening of a portion of the iris without the least trace of relaxation in the tone of the sphincter border.

These facts, when taken in conjunction with the histological details to which attention has already been directed, warrant the assumption that the presence of a definite dilator pupillæ muscle has been established.

The *posterior limiting lamella* has been the subject of considerable confusion in the description of the posterior border of the iris-stroma as given by various authors: this has been due largely to the uncertainty as to the

[1] Langley and Anderson: On the Mechanism of the Movements of the Iris, Journal of Physiology, vol. XIII., 1892.

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relations and significance of the stratum of spindle-cells which have been already described. These elements, in the light of our present knowledge, must be regarded, for the reasons already presented, as representing a contractile sheet, which is accepted by many, including the writer, as the expression of a distinct dilator pupillæ muscle. While the more or less perfect layer of spindle-cells is intimately united with the structure forming the posterior boundary of the iris-stroma, critical examination of suitably prepared sections shows that the spindle-cells are separated from the posterior pigmented zone by a stratum of great delicacy,—the posterior limiting lamella proper.

This last-named structure, also called the posterior boundary lamella, the vitreous lamella, the basal membrane, or the membrane of Bruch, appears as a clear lamella of great tenuity, its maximum thickness not exceeding .002 millimetre, which closely adheres to the outer stratum of the pigmented retinal zone behind and is intimately related to the sheet of spindle-cells in front. The almost homogeneous appearance of the limiting lamella under moderate amplification gives place to a distinct, though delicate, radial striation when examined with high powers. After prolonged maceration, according to Schwalbe,[1] the striated lamella breaks up into fine stiff fibrillæ, entirely distinct from muscle-fibres. The intimate union of the lamella with the subjacent pigmented tissue not infrequently results in the adherence of portions of the outer retinal layer to the lamella, in consequence of which oval nuclei and particles of the pigmented cells remain attached to and seemingly form constituents of the limiting membrane.

The posterior limiting lamella of the iris may probably be regarded as the anterior continuation of the membrane of Bruch, as found in the ciliary zone and posterior parts of the choroidal tract; in constitution it is the result of a local condensation of the connective-tissue stroma, and corresponds to a membrana propria in other locations. The recognition by Merkel[2] of the posterior limiting lamella as distinct from the superimposed stratum of spindle-cells has been recently[3] reaffirmed by him; the existence of the limiting lamella is also admitted by Schäfer;[4] Retzius,[5] on the contrary, seems to consider the dilator stratum and the membrane of Bruch as inseparable.

The *pigmented layer* covering the posterior surface of the iris as far as the anterior margin of the pupillary opening, while constituting anatomically an integral part of the diaphragm, possesses a distinct morphological value, since it represents the remains of the anterior limits of the ectodermic secondary optic vesicle.

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[1] Schwalbe: Anatomie der Sinnesorgane, S. 206.

[2] Merkel: Handbuch der topograph. Anatomie, Bd. I., 1887, S. 256.

[3] Merkel: Ergebnisse der Anatomie u. Entwickelungsges., Bd. III., 1893 (Anmerkung, S. 287).

[4] Schäfer: Quain's Anatomy, 10th ed., vol. III., Pt. 3, 1894, p. 33.

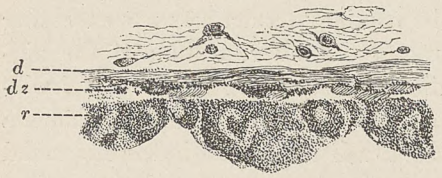
[5] Retzius: Zur Kenntniss vom Bau der Iris, Biolog. Untersuch., Neue Folge, v., 1893.

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The deeply colored posterior zone in suitable preparations is shown to consist of two distinct layers,—an outer, composed of low, irregular spindle-cells, and an inner, made up of short, cylindrical, polygonal elements. These layers represent the outer and inner lamellæ of the embryonal optic cup, and at their extreme anterior limits, corresponding to the front margin of the pupil, they become continuous, as in their earlier stage of development.

The *outer layer* consists of a single row of deeply pigmented fusiform elements, about .070 to .080 millimetre in length and .009 to .010 millimetre in thickness, the general disposition of which is radial, and closely follows the minute inequalities of the posterior boundary layer with which these cells are almost inseparably united. The unbroken investment thus formed is continuous at the ciliary border of the iris with the low columnar or polyhedral pigmented elements constituting the outer lamella of the pars ciliaris retinæ; at this point the radial arrangement of the spindle-cells gives place to a more circular disposition. At the pupillary margin the low, irregular cells of the outer layer pass directly into the densely pigmented elements of the posterior layer, the two strata being directly continuous.

Fig. 45.



Radial section of posterior portion of human iris. (Retzius.)—*d*, dilator fibres; *dz*, *r*, anterior and posterior layers of retinal zone. Magnified about 400 diameters.

The *inner layer* consists of cells in which the pigment particles are so crowded that ordinarily all demarcation between the individual elements is obscured, the layer appearing as one continuous and unbroken pigmented zone. Favorable preparations, as afforded by albino eyes, or after the removal of the color by means of bleaching solutions, conclusively show that this layer consists of short columnar or polygonal elements, .030 to .035 millimetre in thickness, the boundaries of which are sharply defined when not obscured by the usual dense accumulation of pigment granules. The cells likewise possess spherical nuclei. The dimensions of these elements, as well as of those of the outer layer, are evidently largely influenced by the contraction and dilation of the pupil, in which variations the cells of the pigment layer are entirely passive.

At the ciliary border of the iris the cells of the posterior layer are directly continuous with the elements which constitute the inner stratum of the pars ciliaris retinæ; the pigment particles become less closely aggregated and gradually abandon the innermost portion of the cells.

The inner surface of the pigment layer is covered by an extremely delicate membrane of a homogeneous cuticular character, the *limitans iridis*, which, as suggested by Schwalbe, is probably the continuation of the similar cuticular investment of the pars ciliaris retinæ. Its great delicacy, and the

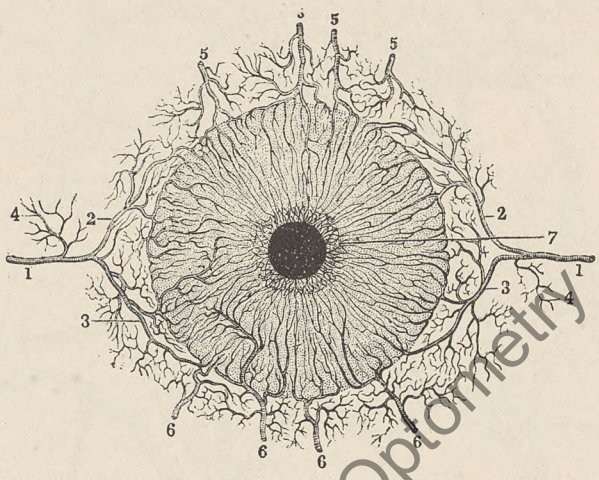
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readiness with which it splits and becomes separated from the iris, account for the quite common absence of the membrane in usual preparations.

The Blood-Vessels of the Iris.—The *arteries* supplying the iris are given off from the anterior border of the *circulus arteriosus iridis major*, which, as already stated, is situated within the ciliary region immediately around the outer margin of the iris. The iridial branches thus originating spring from points which closely correspond to the attachments of the ciliary processes to the iris, several vessels, however, not infrequently arising within the area belonging to a single process. (Leber.)

The radially disposed arterial stems proceed through the stroma layer as far as the outer border of the pupillary zone, giving off branches at acute angles during their course; on reaching the sphincter zone they freely inos-

FIG. 46.



Arterial supply of the iris. (Sappey.)—1, 1, long ciliary arteries giving off their superior (2, 2) and inferior (3, 3) branches; 4, 4, recurrent branches to choroid; 5, 5, 6, 6, anterior ciliary arteries; 7, network surrounding pupil.

culate with one another and with their branches to form a second annular anastomotic circuit, the *circulus arteriosus iridis minor*, which lies near the anterior surface of the iris and, during fœtal life, communicates with the vascular pupillary membrane.

The lesser arterial circle distributes branches in three directions: an inner set continues towards the pupillary margin, to break up into a capillary net-work within the sphincter muscle, a posterior group contributes a capillary net-work occupying the posterior surface of the stroma layer, and a third anterior set provides a capillary reticulum which ramifies within the anterior boundary layer.

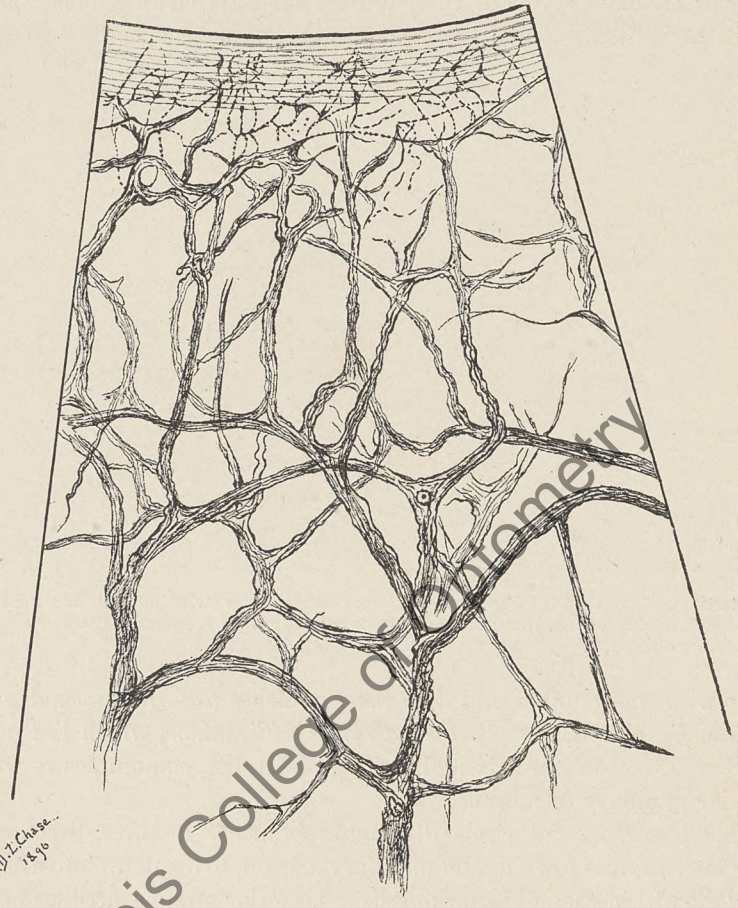
These capillaries become tributary to venous radicles which pursue a general radial course directed towards the ciliary border; the veins thus arising unite at acute angles to form vessels which are continued as venous trunks along the inner surface of the ciliary muscle, in company with the

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veins from the ciliary processes, and finally empty into the large venæ vorticosæ.

In structure, the arteries of the iris-stroma are characterized by a relative preponderance of elastic tissue and meagreness of muscular elements; they possess, as do also the veins, a robust adventitious sheath, contributed by the condensed surrounding iris-stroma, in which stellate cells are often conspicuous. According to Michel,[1] the vessels of the iris are provided with an additional endothelial sheath, which thus partially lines the perivascular lymph-space situated within the thickened adventitious coat.

Fig. 47.



General surface view of the distribution of the motor nerves of the iris of rabbit after injection of the living animal with methylene-blue. (Hosch.)—As a matter of convenience, many of the minute twigs within the sphincter border have not been represented. Magnified 70 diameters.

The Lymphatics of the Iris.—Distinct lymphatic vessels do not exist within the iris, the absorbent system being represented by the lymph-spaces within the stroma layer.

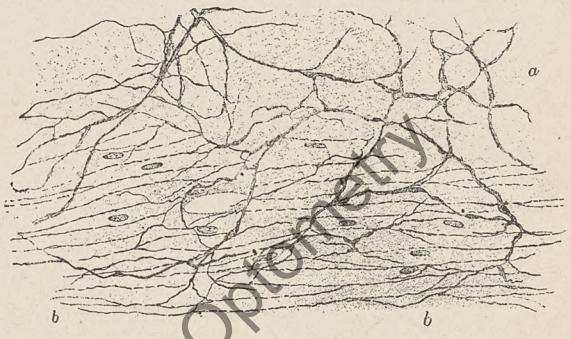
[1] Michel: Die histologische Structur des Irisstroma, 1875.

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These interfascicular lymphatic clefts, which occur in such profusion in all parts of the iris that the entire stroma layer possesses the character of a sponge-like tissue, constitute a freely intercommunicating system of spaces. The tissue-juices contained within the lymphatic channels are carried towards the periphery of the iris, at which position the iridial spaces, in addition to communicating with the interstitial clefts within the ciliary body, probably communicate with the intra-pectinate spaces of Fontana, as maintained by Schwalbe.

The question as to the occurrence of direct absorption of the aqueous humor through the anterior surface of the iris has been both affirmatively and negatively answered, but the recent careful investigations of Tückermann[1] render the probability of such absorption very questionable, and, at best, only to the very limited extent to which it takes place through the posterior surface of the cornea. In both situations particles within the aqueous humor may be taken up by the protoplasm of the endothelial cells. The loose character of the stroma and the particularly rich vascular supply fully suffice to account for the contents of the lymph-spaces of the iris without assuming a participation of the fluids within the anterior chamber; the only communication between the latter cavity and the iridial channels is the indirect path by way of the spaces of Fontana.

FIG. 48.



Surface view of sphincter muscle of iris of rabbit after gold staining. (Meyer.)—*a*, plexus of pale nerve-fibres which become continuous at *b* with intermuscular fibrillæ. High amplification.

The Nerves of the Iris.—The classic paper of Arnold, together with the subsequent contributions of Faber, Pause, Formad, Meyer, Fürst, and Eversbusch, forms the basis of our knowledge concerning the distribution of the nerves within the iris.

The nerve-trunks supplying the iris proceed inward from the annular intra-muscular plexus, the *orbiculus gangliosus*, formed by the ciliary nerves within the muscle of accommodation. The nervous stems, which are at first composed principally of medullated fibres and pursue a spiral course, pass into the ciliary border of the iris, and upon entering the stroma layer divide into branches which are united and rearranged to constitute plexuses of various character. In the disposition of the principal nerve-trunks there seems to be no close correspondence between their course and that of the blood-vessels.

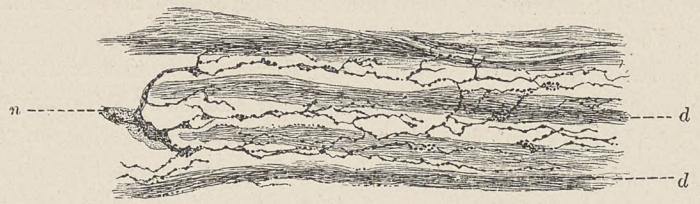
[1] Tückermann: Ueber die Vorgänge bei der Resorption in die vordere Kammer injizierter körniger Farbstoffe, Archiv f. Ophthalmol., Bd. XXXVIII., 1892.

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According to Meyer,[1] the iridial nerves provide nerve-endings of three kinds: 1, motor endings within the muscular tissue; 2, sensory endings within the superficial layers of the stroma; 3, vaso-motor endings in the walls of the arteries and the capillaries.

The fibres destined for the supply of the muscular tissue, after forming

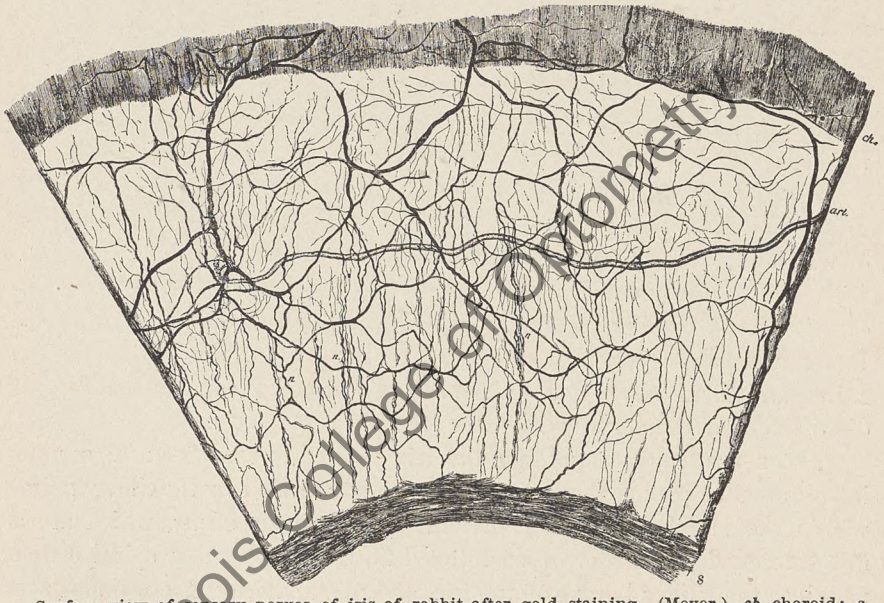
FIG. 49.



Horizontal section of rabbit's iris after staining with gold, showing motor nerve-endings in dilator layer. (Retzius.)—*d*, *d*, muscle-fibres; *n*, nerve breaking up into intermuscular fibrillæ. Magnified about 950 diameters.

a coarse mesh-work as they journey towards the pupillary zone, break up into smaller non-medullated twigs, which unite at the outer border of the sphincter muscle to form an annular pupillary plexus. Numerous delicate non-medullated fibres pass from the latter into the muscular tissue, within

FIG. 50.



Surface view of sensory nerves of iris of rabbit after gold staining. (Meyer.)—*ch*, choroid; *s*, sphincter pupillæ; *art*, circulus arteriosus iridis major; *n*, spirally coursing nerves. All nerves represented are medullated; others have been omitted. Magnified 7 diameters.

which they sooner or later break up into the attenuated ultimate fibrillæ for the supply of the individual muscle-cells between which the nerve-

[1] Meyer: Die Nervendigungen in der Iris, Archiv f. mik. Anat., Bd. XVII., 1880.

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filaments end. The ultimate fibrillæ correspond in their course with the general disposition of the muscular tissue, present varicosities, and terminate in free endings between the contractile elements. It is a significant fact in connection with the determination of the character of the spindle-cells of the posterior lamella of the iris-stroma that Retzius[1] has discovered definite motor nerve-endings within this layer.

The sensory nerves of the iris form an extensive superficial plexus of largely medullated fibres within the anterior plane of the stroma layer. The terminal part of this sensory plexus is composed of non-medullated fibres of especial delicacy, which lie close beneath the anterior endothelium.

The vaso-motor nerves are represented by the delicate bundles of non-medullated fibres which accompany the blood-vessels and terminate in free endings within the muscular tunic of the arteries, or in pale fibres entwining the capillaries.

The existence of ganglion-cells within the iris has been a subject of conflicting opinion. Among those who have described nerve-cells as present in this situation are Arnold and Faber, while Pause, Iwanoff, Formad, Fürst, and Schwalbe have denied their existence. Meyer[2] records having found in the human iris small multipolar cells which, while possessing apparently no connection with the nerve-fibres, strongly resembled in their general appearance ganglion-cells. Hosch,[3] likewise, describes small (.012 to .015 millimetre in diameter) multipolar elements within the sphincter zone of the human iris, which not only are identical in appearance with ganglion-cells, but are directly connected with the nerve-fibres. These instances of the direct observation of the nerve-cells, it will be noted, pertain to human tissue; both Meyer and Hosch agree with the majority of investigators in denying the presence of ganglion-cells within the rabbit's iris, which has been the usual subject of observation. While admitting the possible presence of small nerve-cells along the course of the fibres taking part in the formation of the pupillary plexus, it is certain that their number and size are so insignificant that the usually accepted doctrine, that the iris is without ganglion-cells, may be still regarded as true.

THE NERVOUS TUNIC.

The nervous tract of the eyeball consists essentially of the highly differentiated expansion of the optic vesicle and its cerebral extension, the direct derivatives of the neural ectoderm, which form the retina and parts of the optic nerve. Regarded in the light of the newer views concerning the retina, as based upon the investigations of Tartuferi, Golgi, Cajal, Dogiel, Retzius, van Gehuchten, His, and others, this tunic of the eyeball can no longer be placed in the same category with the remaining coats, but

[1] Retzius: Zur Kenntniss zum Bau der Iris, Biolog. Untersuch., Neue Folge, v., 1893.
[2] Meyer: loc. cit.
[3] Hosch: Ehrlich's Methylenblaumethode und ihre Anwendung auf das Auge, Archiv f. Ophthal., Bd. xxxvii., 1891.

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must be conceded a morphological position of far greater dignity and importance. The retina must be considered as a true nervous centre and as a peripherally situated portion of the central nervous system rather than as merely the complex percipient apparatus of light-stimulus.

The retinal tract in its entirety, as representing the structures evolved from the optic vesicle, extends from the entrance of the optic nerve posteriorly as far forward as the anterior margin of the pupillary margin. This extensive sheet, from the profound variations which certain of its parts undergo both in structure and in function, becomes differentiated into two sharply contrasting segments. The posterior of these, extending from the optic entrance to the ora serrata, and embracing about two-thirds of the eyeball, constitutes the actively functionating nervous centre, the retina proper; the anterior segment continues from the ora serrata over the posterior surface of the ciliary body and the iris as far forward as the anterior pupillary margin, and is known under the names of *pars ciliaris* and *pars iridica retinæ*, the representatives of the rudimentary anterior portions of the two layers of the optic cup.

The retina proper, or *pars optica retinæ*, consists of an inner and an outer lamina, which correspond to the very unequally developed inner and outer layers of the optic vesicle. The outer lamina includes the pigment layer alone, while to the inner lamina belong all the remaining layers of the fully formed retina. The inner lamina permits of further subdivision of its structures, as suggested by Schwalbe, into the *neuro-epithelial* and the *cerebral* layer.

The relations of these divisions to the individual retinal layers may be expressed as follows:

I. Outer Layer of Optic Vesicle.	*Pigment layer.*	*A.* Pigment layer.
	Layer of rods and cones.	*B.* Neuro-epithelial layer.
	Layer of bodies of visual cells (outer nuclear layer).	
II. Inner Layer of Optic Vesicle.	*External plexiform layer* (outer reticular layer).	*C.* Cerebral layer.
	Layer of bipolar cells (inner nuclear layer).	
	Internal plexiform layer (inner reticular layer).	
	Layer of ganglion-cells.	
	Layer of optic nerve-fibres.	

The retina, in common with other parts of the central nervous system, consists of two varieties of elements, the nervous and the sustentacular. The latter constitute the supporting neuroglia which appears as a reticular framework composed of columnar segments, the long fibres of Müller, which extend the entire thickness of the retina, and by apposition of their expanded outer and inner extremities produce the seemingly continuous structures known as the external and internal limiting membranes.

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While the advances in the comprehension of the structural details of the retina will ever be deeply indebted to the classic investigations of Heinrich Müller, Max Schultze, Kölliker, Krause, W. Müller, Schwalbe, and others, the close of the last decade left still much uncertainty concerning the exact mode of transmission of the light-stimuli from the percipient elements to the nervous centres.

The almost simultaneous introduction of the chrome-silver impregnation method of Golgi,[1] as presented in his later and more important communication, and the methylene-blue staining of Ehrlich,[2] supplied a marked impetus to renewed investigations of the nervous system which have borne fruit in the many important advances made in our knowledge of the form and relations of the nervous elements. As was to be expected, the capabilities of these recent methods were soon taken advantage of in renewed study of the retina, the intricate structure of which has always remained an inviting field for the foremost histologists.

A new epoch in the anatomy of the retina was inaugurated by the appearance of Tartuferi's[3] paper, in 1887, recording the results of his application of the Golgi silver staining to that structure. These investigations were immediately followed by those of Dogiel,[4] in which the discoveries yielded by the use of the methylene-blue stainings were communicated. The first of the brilliant researches of Ramon y Cajal[5] was announced almost at the same time. The years intervening since the publication of these important papers have witnessed great activity in the investigation of the nervous elements of the retina, as evidenced by the appearance of an extended series of communications by the authors just named, as well as of the contributions by Baquis,[6] Fromaget,[7] Retzius,[8] and others.

The interest and importance of these observations, particularly those of Golgi and of Cajal, lay not only in the decided advance in the more accurate knowledge of the relations of the nervous elements of the retina, but in the establishment of the broader theorem of the independence of nerve-cells and their extensions as axis-cylinders in general. Upon the evidence advanced by the labors of these investigators, as well as by their

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[1] Golgi: Sulla fina anatomia degli organi centrali del sistema nervosa, 1885, which was preceded ten years by his first paper, Sulla fina structura dei bulbi olfactorii, 1875.

[2] Ehrlich: Ueber die Methylenblaureaktion der lebenden Nervensubstanz, Deutsch. med. Wochenschr., No. 4, 1886.

[3] Tartuferi: Sulla anatomia della retina, Archivio per le scienze mediche, vol. XI., 1887; and Internat. Monatsschrift für Anat. u. Physiolog., Bd. IV., 1887.

[4] Dogiel: Ueber das Verhalten der nervösen Elemente in der Retina der Ganoiden, Reptilien, Vögel und Säugethiere, Anatom. Anzeiger, Bd. III., 1888.

[5] Ramon y Cajal: Estructura de la retina de las aves, Revista trim. de Histología normal, 1888.

[6] Baquis: Sulla retina della faina, Anatom. Anzeiger, Bd. V., 1890.

[7] Fromaget: Contribution à l'étude de l'histologie de la retina, Archiv. d'ophthalmol., t. XII., 1892.

[8] Retzius: Ueber die neueren Prinzipien in der Lehre von den Einrichtungen des sensiblen Nervensystems, Biolog. Untersuch., Neue Folge, IV., 1892.

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own supplementary confirmatory studies, many of the foremost authorities, including Kölliker, His, v. Lenhossék, Retzius, and others, accept the view that every nerve-cell exists as an independent individual element, and neither ends in net-works formed by its own ramifications joining with those of other cells, nor communicates by actual union with other cells. Direct anatomical continuity between nervous elements, therefore, is no longer accepted, contiguity, as represented by approximation and contact, being regarded as the closest relation into which such elements enter. Although accepted by the majority of anatomists at present, it should be mentioned that direct contiguity between certain elements is still maintained by some authorities, among whom Dogiel, Waldeyer, and Merkel are conspicuous.

FIG. 51.

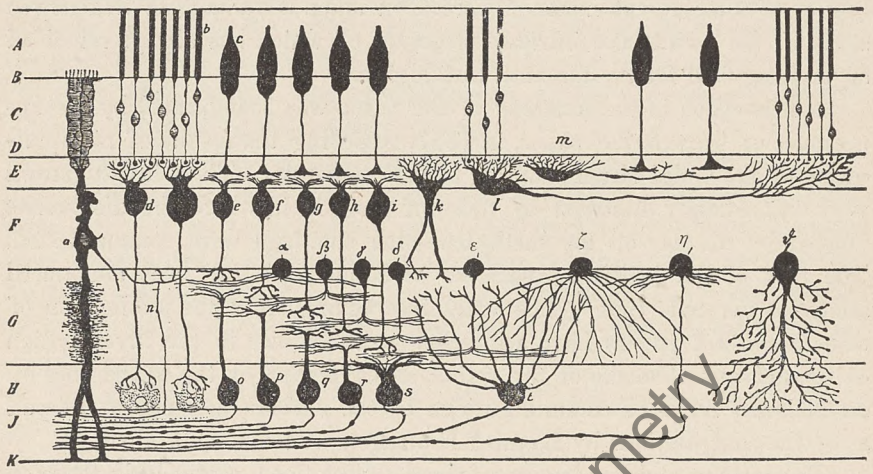


Diagram illustrating the relation of the retinal elements. (Kallius.)—*A*, layer of rods and cones; *B*, limitans externa; *C*, outer nuclear layer (bodies of visual cells); *D*, Henle's external fibrous layer (composed principally of rod-fibres); *E*, outer plexiform layer; *F*, inner nuclear layer (rod and cone bipolars); *G*, inner plexiform layer; *H*, layer of large ganglion-cells; *J*, fibre-layer; *K*, limitans interna; *a*, supporting fibre of Müller; *b*, *c*, rod and cone visual cells; *d*, bipolars belonging to rod-cells; *e–i*, bipolars belonging to cone-cells; *k–m*, horizontal nerve-cells; *n*, centrifugal nerve fibre; *o–t*, ganglion-cells connected with optic fibres; *α–ε*, amacrines arranged in layers; *ζ–ϑ*, diffuse amacrines; *η*, nervous amacrine.

The fanciful conceptions of the structure of the retina advanced by Johnson[1] can hardly be considered seriously.

The application of the Golgi silver staining, particularly in the modified methods introduced by Cajal, has been of especial importance in revealing the nature and relations of many retinal elements which before were obscure. Before proceeding to the detailed consideration of the individual elements composing the retina, a general sketch of the anatomy of this complicated nervous sheet, based upon the newer accepted views, will be of advantage. This purpose will be served by a study of the accompanying diagram illustrating the present views concerning the structure of the retina

[1] Johnson: Observations on the Macula Lutea, Archives of Ophthalmology, vol. XXIV. 3, 1895; ibid., vol. XXV. 1, 1896.

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which has been prepared by Kallius[1] in accordance with the observations of Ramon y Cajal.

Passing from the outer or choroidal surface towards the inner boundary of the retina, ignoring the pigment layer, the first two strata, which constitute the neuro-epithelial layer, are occupied by the external and internal parts of the visual cells. The former comprises the layer of rods and cones, the latter the external nuclear layer, of the older nomenclature. It will be noticed that the central or inner terminations of the visual cells are not limited to the neuro-epithelial layer, but pass for a short distance within the subjacent outer plexiform or reticular stratum.

Within the latter zone the two forms of visual cells end in a somewhat different manner; the rod-cells terminate in knob-like expansions which are embraced by the arborescent processes of the bipolar nerve-cells of the outer ganglionic (inner nuclear) layer. The centrally directed axis-cylinder processes of these bipolar cells pass as far as the inner ganglionic layer, where they end in arborizations surrounding the large ganglion-cells.

The inner terminations of the cone-cells within the outer plexiform layer are more expanded than those of the rods, and also give off a few short lateral processes. The bases of the cone-cells come into intimate relation with the ramifications which proceed from the bipolar cells of the outer ganglionic layer.

It will be noted that the centrally coursing axis-cylinder processes of the last-mentioned cells are confined to the inner plexiform zone, but that all do not reach the same level, some breaking up into the terminal ramifications immediately after entering the zone, while others pass to various levels within the same layer. The cone ganglion-cells, therefore, map out a series of secondary zones of progressively deeper level. The central expansions of the bipolar ganglion-cells of the cones come into close relation with the arborizations of the large nerve-cells of the inner ganglion layer. The cone- and the rod-cells are, therefore, in relation with bipolar ganglion-cells which are of two kinds, each form of visual cell having relations with a distinct nervous element.

The axis-cylinders of the large cells of the inner ganglion layer are continued brainward as the fibres of the optic nerve. The presence, however, of "centrifugal" fibres which extend outward as far as the outer boundary of the inner plexiform layer has been demonstrated.

In addition to the foregoing relations of the more important retinal elements which thus constitute a direct pathway for the conveyance of impressions received by the visual cells, the recent studies of the retina have discovered the existence of numerous additional elements which probably establish paths for the indirect transmission of impressions.

The elements in question include the horizontal or basal cells found in the external plexiform layer the processes of which ramify about the extremi-

[1] Kallius: Ergebnisse der Anatomie und Entwickelungsgesch., Bd. II., 1892, S. 251.

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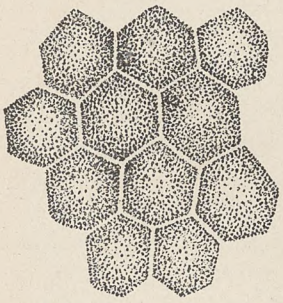
ties of the visual cells, sometimes, however, extending centrally as far as the internal plexiform zone. Additional elements are encountered within the inner plexiform layer, as the various spongioblasts or "amacrine cells" of Cajal. Three varieties of these elements have been described: *a*, those which, as the "layered" spongioblasts, extend to various depths within the plexiform layer, and there end by dividing into ramifications which possess a generally horizontal disposition; *b*, those which, as the "diffuse" spongioblasts, possess large bodies and send off more or less elaborate arborizations into the plexiform, and partly also the inner ganglion, layer; and, *c*, those which, as the "nervous" spongioblasts, possess a recognizable axis-cylinder extending into the fibre-layer.

The sustentacular elements of the retina are contributed by the complicated and irregular fibres of Müller, which pass from the layer of rods and cones through the retinal strata to form the innermost boundary of the nervous sheet; in their course they enter the several strata and give off secondary ramifications which supply the tissue supporting the cells of the individual retinal layers.

The general arrangement and relations of the retinal elements having been broadly sketched, a more detailed consideration of the individual layers and their component elements claims further attention.

The Pigment Layer.—Reference to the section on the Development of the Eye will show that the pigment layer is the direct and sole representative of the outer lamella of the optic cup, and therefore corresponds to that segment of the primary optic vesicle which has not suffered invagination. The outer layer very early evinces the disposition to remain thin and to become pigmented, the accumulation of colored particles first taking place near the anterior lip of the optic cup and extending towards the posterior pole.

Fig. 52.



Surface view of pigmented retinal epithelium. Magnified 500 diameters.

The layer of retinal pigment in the fully developed eye consists of a single stratum of nucleated polygonal cells the protoplasm of which, when seen in surface views, is almost completely filled with colored particles, with the exception of the nuclear areas. The cells are usually hexagonal in outline, but numerous exceptions are observed in which the number of sides is reduced to four or five; on the other hand, as shown by Boden and Sprawson,[1] they may be increased to seven or even to ten. The ordinary diameter of the pigment-cells varies between .012 and .018 millimetre, here and there groups of smaller cells being interspersed, or, on the contrary, isolated cells of unusual size being

[1] Boden and Sprawson: The Pigment-Cells of the Retina, Quart. Jour. of Mic. Science, vol. xxxiii., 1892.

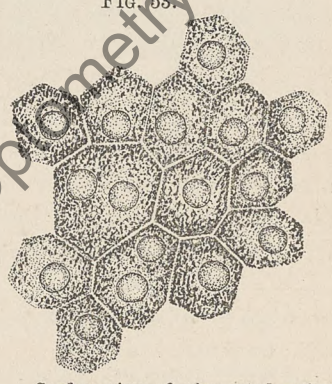
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surrounded by smaller ones. In the immediate vicinity of the ora serrata the pigmented elements are of exceptionally large size throughout a zone 1 to 1.5 millimetres in breadth, in which, as pointed out by Kuhnt,[1] the cells are so much more deeply colored than those of the centrally situated areas that a difference in the general tint of the peripheral zone is noted with the unaided eye. The large cells of this deeply colored zone possess nearly always more than six sides, and very frequently have more than a single nucleus.

Surface views give the impression that the entire cell, with the exception of the nucleus, contains pigment; that such, however, is not the case is shown by vertical sections, in which it is seen that each cell consists of three parts,—an outer zone, containing the nucleus, wanting in pigment and presenting a smooth surface towards the choroid; a middle zone, deeply pigmented and sometimes known as the "base" of the cell; and an irregular inner zone, consisting of indefinite protoplasmic processes which extend between the outer segments of the visual cells, whose ends are thus received within the pigment layer. According to Kuhnt[2] and others, the outer surface of the pigment-cells possesses a delicate keratose cuticle which also invests the sides of the closely approximated cells, and appears in surface views as the clear boundary lines defining the deeply colored hexagonal areas.

In many of the lower animals, as certain fishes, amphibians, and birds, the outer zone of the pigment-cells contains foreign, and sometimes brightly colored, substances, of which aleuronoid particles and fat droplets are the most frequent. Angelucci,[3] who has carefully studied these inclusions, states that the aleuronoid particles are absent in the retinal cells of mammals, but that exceptionally, as in the rabbit and the ox, oil droplets may exist. None of these foreign particles, however, have been observed within the human retina. The investigations of Kerschbaumer[4] show that in many cases decrease of the retinal pigmentation, particularly within the extreme anterior zone in the vicinity of the ora serrata, accompanies other senile changes within the eye. The source of the color within the retinal epithelium is the blood, from which the substances, in a condition of solu-

FIG. 53.



Surface view of pigmented retinal epithelium from an aged subject. The cells exhibit loss of pigmentation and multiple nuclei. Magnified 500 diameters.

[1] Kuhnt: Grosszellenzone im Pigmentepithel des Menschen, Bericht über d. 12. Versamml. d. ophthalmol. Gesellsch. in Heidelberg, 1879.

[2] Kuhnt: loc. cit.

[3] Angelucci: Histologische Untersuchungen über das retinale Pigmentepithel der Wirbelthiere, Archiv f. Anat. u. Physiologie, 1878.

[4] Kerschbaumer: Über Altersveränderungen der Uvea, Archiv f. Ophthalmol., Bd. XXXVIII., 1892.

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tion, are deposited within the protoplasm of the cells; in this connection, as pointed out by Scherl,[1] the fact is suggestive that the first deposit of retinal pigment occurs in close relation to the earliest vascular supply of the interior of the primitive organ. While Scherl failed to find iron in the coloring-matter, Mays,[2] by the use of a mixture of a ten per cent. solution of hydrochloric acid and a five per cent. solution of potassium sulphocyanide, succeeded in obtaining a characteristic iron reaction.

The pigment granules occur in the form of minute crystals, their long axes being placed generally at right angles to the retinal free surface. The distribution of the pigment within the protoplasm during life, moreover, is by no means constant, but varies greatly according to the intensity of light-stimulus to which the tissue is subjected..

The researches of Kühne and Sewall,[3] Angelucci,[4] Englemann,[5] Gradenigo,[6] v. Genderen-Stort,[7] Fick,[8] and others leave little doubt that the elements of the retinal epithelium undergo marked change during exposure to light. Under such stimulus the pigment particles advance along the protoplasmic extensions of the epithelial cells between the rods and cones until the outer segments of the visual cells are buried within the pigment. After prolonged exclusion of light, on the contrary, the pigment particles are withdrawn from the processes and become once more aggregated within the basal portion of the cells.

It has been shown that the migration of the pigment particles is not effected by the protrusion or retraction of the protoplasmic processes themselves, but is due rather to the displacement of the particles by currents streaming within the cell protoplasm, somewhat similar to the transportation of granules within the pseudopodia of the amœba.

In addition to the migration of the pigment particles along the protoplasmic extensions of the epithelium, Englemann and v. Genderen-Stort observed that conspicuous changes in the elements of the percipient layer also marked the effect of light-stimulus. These alterations consist particularly in the shortening of the inner cone-segment so that the entire cone

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[1] Scherl: Einige Untersuchungen über das Pigment des Auges, Archiv f. Ophthalmol., Bd. XXXIX., 1893.

[2] Mays: Ueber den Eisengehalt des Fuscins, Archiv f. Ophthalmol., Bd. XXXIX., 1893.

[3] Kühne and Sewall: On the Physiology of the Retinal Epithelium, Journal of Physiology, vol. III., 1879.

[4] Angelucci: De l'action de la lumière et des couleurs sur l'epithelium retinum, Soc. de Méd. de Gand, t. LX., 1882.

[5] Englemann: Ueber Bewegungen der Zapfen und Pigmentzellen unter dem Einfluss des Lichtes und des Nervensystems, Pflüger's Archiv, Bd. XXXVI., 1885.

[6] Gradenigo: Ueber den Einfluss des Lichtes und der Wärme auf die Retina des Frosches, Allgemein. Wiener med. Zeitg., No. 28, 1885.

[7] v. Genderen-Stort: Ueber Form- und Ortsveränderungen der Netzhautelemente unter Einfluss vom Licht und Dunkel, Archiv f. Ophthalmol., Bd. XXXIII., 1888.

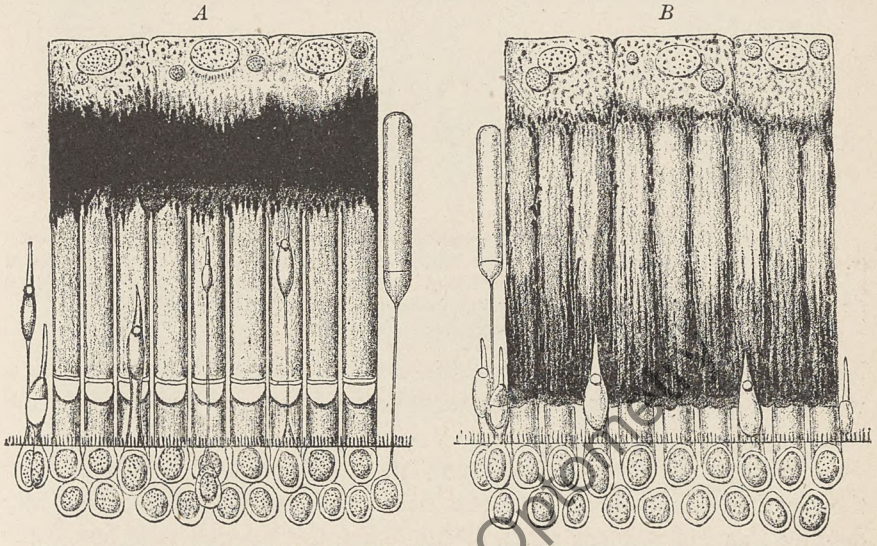
[8] Fick: Untersuchungen über die Pigmentwanderung in der Netzhaut des Frosches, Archiv f. Ophthalmol., Bd. XXXVII., 1891.

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lies nearer to the external limiting membrane, the shortening depending upon the contraction of the protoplasmic part of the cone which connects the cone-granule with the ellipsoid.

Associated with the foregoing alterations in the position of the pigment and the relations between the percipient elements and the retinal epithelium, a variation is to be noted in the intimacy of attachment between the pigment layer and the remaining portions of the retina. With the withdrawal of the pigment from between the visual cells, the attachment between the percipient and the pigmented layer of the retina seemingly becomes weakened and the tendency for the two lamellæ to separate more marked. In eyes subjected to the action of light just before death, and

FIG. 54.



Sections of frog's retina, showing the effect of the action of light and of darkness upon the pigment-cells and upon the rods and cones. (v. Gendern-Stort.) Nitric acid preparations. Magnified 600 diameters.—*A*. Pigment and neuro-epithelium after remaining forty-eight hours in absolute darkness. The pigment is collected within the outer nucleated part of the cells; the cones are greatly elongated. *B*. Pigment and neuro-epithelium after five hours' exposure to daylight. The pigment has migrated nearly to the bases of the rods, and the cones have retracted almost to the outer limiting membrane.

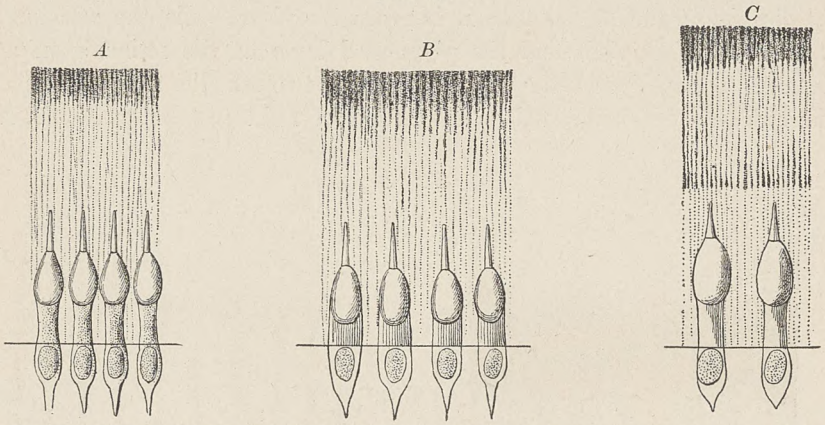
rapidly fixed, the pigment and remaining retinal strata are intimately attached, while in eyes treated in an identical manner after death, but protected from light before, the connection between the pigment and other parts of the nervous coat is but slight; the retina, when removed from eyes so treated, is but imperfectly covered by pigmented cells, since the majority of these remain adherent to the choroid.

The primary cleft between the outer and inner lamellæ of the embryonic optic vesicle does not undergo complete obliteration, but is represented by the interspaces between the rods and the cones and the processes extended from the pigmented cells. These intervals are occupied by a clear, probably fluid, substance (Schwalbe) which may be regarded as a modified lymph,

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since substances injected beneath the pial sheath of the optic nerve sometimes find their passage into the space between the pigment layer and the rods and cones. This fact is regarded by Schwalbe as positive evidence of the communication between the subpigmentary space in question and the central lymph-tracts, a relation partially anticipated by the early continuity

FIG. 55.



Sections of retinæ, showing the effect of exposure to light and darkness on the pigment and cones. (v. Genderen-Stort.) Nitric acid preparations. Magnified 870 diameters.—*A*, Cones from the retina of pig kept in absolute darkness for twenty-four hours. *B*, Cones from the retina of pig exposed to light for two hours. *C*, Cones from human retina kept in darkness for fourteen hours before death.

between the optic vesicle and the brain-cavities. Gifford,[1] likewise, finds a well-developed lymph-space between the retinal pigment and the rods and cones.

The Layer of Neuro-Epithelium.—The neuro-epithelial layer comprises the *visual cells* in their entirety, and hence includes two zones frequently described as independent strata of the retina, the layer of rods and cones and the outer nuclear layer. Since the former of these represents the highly specialized outer portion and the latter the bodies of the visual cells, convenience alone justifies the retention of their recognition as distinct strata, both belonging to the layer constituted by the light-stimulus-perceiving elements.

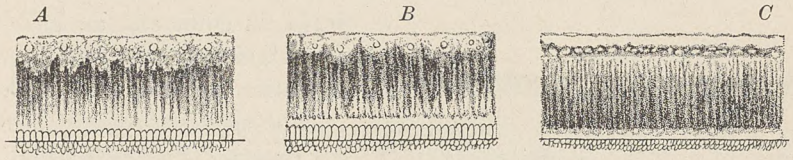
The *layer of rods and cones*, about .060 millimetre in thickness, therefore embraces the outer parts of the two kinds of visual cells. Although differing in their details, the rods and cones possess many points in common. Each consists of an inner and an outer segment, of which the former is the greater in diameter, especially in the cones. The position of juncture between the segments in general corresponds about to the middle of the entire stratum, although the outer portions of the rods, which constitute about half of the entire length of these structures, embrace a greater

[1] Gifford: Weitere Versuche über die Lymphströme und Lymphwege des Auges, Archiv f. Augenheilkunde, Bd. XXVI., 1893.

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proportion of the depth of the layer than do the corresponding parts of the cones, which are usually much shorter and do not reach the outer limits of the zone. It has been maintained by v. Genderen-Stort,[1] however, that during life the junction between the outer and inner segments of the cones

FIG. 56.

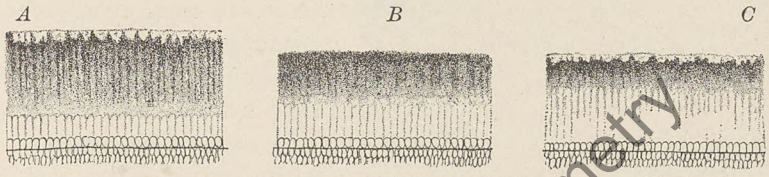


Outer layers of frog's retina, showing the effect of exposure to light for varying periods on the form and position of the elements. (v. Genderen-Stort.)—*A*, after six minutes' exposure to diffuse light; *B*, after thirty minutes' exposure to weak diffuse light; *C*, after thirty minutes' exposure to strong diffuse light.

lies well outward between the outer segments of the rods, and, therefore, farther from the membrana limitans externa than is generally pictured.

The outer segments of the rods are nearly of the same size as the inner, while the outer tapering portions of the cones are much smaller than the

FIG. 57.



Outer layers of frog's retina, showing the effect of darkness on the position and form of retinal elements. (v. Genderen-Stort.)—*A*, after one hour in darkness; *B*, after two hours in darkness; *C*, after four hours in darkness. Maximum retraction of pigment into bases of pigmented cells and about the apices of the cone-pyramids.

expanded conical inner divisions. The outer segments of both rods and cones exhibit well-marked differences from the inner segments in their chemical and optical properties, as shown by their behavior towards stains and refracting powers. The inner divisions stain readily with carmine, hæmatoxylin, iodine, and other coloring solutions, while the outer segments remain unaffected. The latter are doubly refracting, the inner singly refracting, in their action upon light.

Additional structural peculiarities, presently to be described, emphasize the distinction between the outer and the inner segments. The early investigations of Heinrich Müller, Kölliker, Max Schultze, and others during the two decades following the middle of the present century laid the foundation of our present knowledge of the structure of the retina; and, while the results of these achievements have become now so much a part of the common possession of anatomy that a detailed reference to the many

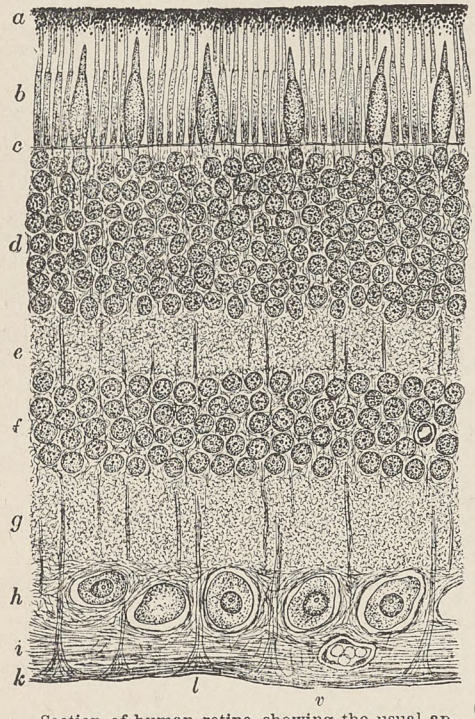
[1] v. Genderen Stort: loc. cit.

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individual papers contributed by these writers seems no longer necessary, every one engaged in a study of the retina will be glad to acknowledge the deep obligations of science to the indefatigable industry of these histologists.

The *rods* of the human retina appear of an elongated, cylindrical form, about .060 millimetre in length and .002 millimetre in diameter, and consist of an outer and an inner division which share almost equally the entire length of the cylinder.

FIG. 58.



Section of human retina, showing the usual appearance of the component layers in ordinary preparations.—*a*, pigment layer; *b*, rods and cones; *c*, external limiting membrane; *d*, outer nuclear layer; *e*, outer plexiform layer; *f*, inner nuclear layer; *g*, inner plexiform layer; *h*, layer of ganglion-cells; *i*, fibre layer; *k*, internal limiting membrane; *l*, base of Müller's fibre; *v*, blood-vessel. Magnified 475 diameters.

The *outer rod-segment*, as usually observed, possesses a uniform diameter and appears as a homogeneous, highly refracting cylinder. Its affinity for the ordinary stains is so slight that it remains colorless after the application of carmine or hæmatoxylin. In many respects this part of the rod must be regarded as corresponding in its nature to a cuticular formation which rests upon the protoplasmic portion of the visual cell represented by the inner segment. High amplification in favorable preparations demonstrates a fine longitudinal striation which has been attributed to the presence of delicate canals. Max Schultze describes additional transverse markings; these he regards as indications of the presence of minute disks, approximately .0006 millimetre in thickness, of which the outer segment is made up. Prolonged treatment with salt and alkaline solutions emphasizes the transverse markings probably by inducing swelling of the cement-substance uniting the disks; in some instances solution of the cement-substance is attended by cleavage resulting in separation and displacement of the disks.

The elaborate investigations of Kühne[1] indicate the presence of a structureless envelope of great delicacy resembling neuro-keratin in nature; the substances—both the disks and the intervening cement—included within

[1] Kühne: various papers in Untersuchungen aus d. physiolog. Institut der Universität Heidelbergs, Bd. II., 1878.

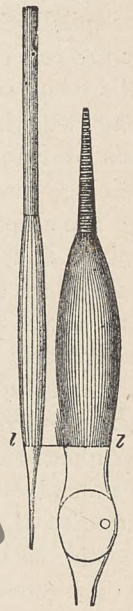
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this investment present in their reactions great similarity, although not identity, to certain parts the coverings of nerve-fibres; they have been, therefore, named "myeloid" by Kühne, as expressing their close relation to the myelin of nerves.

The external segments of the rods possess additional interest on account of being the chief, if not the exclusive, seat of the visual purple or *rhodopsin*, as shown by Boll[1] and Kühne.[2] The visual purple is uniformly distributed through the entire outer segment of the rods, which consequently possess a uniform purplish-red tint. The fovea centralis, when the rods are absent, therefore, is marked as an area devoid of the color presented by other portions of the living retina.

The *inner rod-segment* presents a slightly increased diameter as well as a feebly emphasized elliptical profile, the thickness at the centre being somewhat greater than at either end. Each segment exhibits a differentiation into two parts,—an outer, which appears faintly striated longitudinally and reaches as far as the external division of the rod, and an inner, which retains the finely granular or almost homogeneous character of the cell-protoplasm and seemingly rests upon the external limiting membrane. The outer of these portions of the inner rod-segment, on account of its fibrillar texture, contrasts strongly with the granular structure of the inner division, and is frequently described as the *rod-ellipsoid* (Schwalbe) or the *lenticular body* (M. Schultze). The constancy of this differentiation of the inner segment of the rod is remarkable, since, in a more or less developed condition, it is found in the majority of vertebrate retinæ; in the human and the mammalian eye the rod-ellipsoid is less well defined than in some lower types.

Fig. 59.



Semi-diagrammatic view of a rod and a cone from the human retina. (Max Schultze.)—*l*, *l*, position of the external limiting membrane, below which the nucleated body of the visual cell lies.

The *body of the rod-visual cell* includes that part of the neuro-epithelial element which lies within the outer nuclear layer, through the entire depth of which it extends. It consists of the greatly attenuated protoplasmic column, the *rod-fibre*, and the conspicuous nucleus, the *rod-granule*.

The rod-fibre, at its outer end, is directly continuous with the granular protoplasmic inner division of the internal segment of the rod, while its inner end extends through the entire thickness of the outer nuclear layer a short distance into the outer reticular or plexiform layer. Within this latter stratum the rod-fibre ends in a minute expansion, or end-knob, in close relation with the surrounding and enveloping terminal arborizations

[1] Boll: Zur Anatomie und Physiologie der Retina, Archiv. f. Anat. u. Physiol., Physiol. Abth., 1877.

[2] Kühne: Zur Photochemie der Netzhaut und über den Sehpurpur, Untersuchungen aus d. physiolog. Institut d. Univ. Heidelbergs, Bd. I., 1877.

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of the bipolar nerve-cells which are particularly devoted to the rod-cells. The course of the fibre within the outer nuclear layer is marked by numerous varicosities which give the cell-body an irregular beaded profile; the tendency to the formation of these enlargements appears to be unusually pronounced after the action of diluted solutions of chromic and osmic acid. (Schwalbe.)

The rod-granule, as the nucleus of the rod-visual cells is termed, being of much greater diameter than the fibre, marks the position of a conspicuous spindle-form swelling in which the thin sheet of protoplasm contributed by the cell envelops the elliptical nuclear body. The nuclei of the rod-cells occur at all levels of the outer nuclear zone, a single nucleus being connected with each fibre. Owing to the numerical preponderance of the rods over the cones, they constitute the chief constituents of the deeply staining granules characterizing the stratum.

The elliptical nuclei, from .006 to .007 millimetre in length, when examined under high amplification in favorable preparations, exhibit alternating dark and light cross-stripes. The darker, more deeply staining substance always occupies the poles of the nucleus, the intermediate zone being appropriated by the lighter and faintly coloring material; not infrequently the single light central stripe is subdivided by an additional dark zone; in such cases five instead of three bands are present. Flemming[1] has described the appearance within the nuclei, after treatment with osmic acid, of minute additional bodies which he regards as nucleoli. According to the same authority, the boundaries between the dark and the light bands are not smooth, but uneven and sometimes serrated.

The *cone-visual cells* present the same divisions as do the rod-cells, each being made up of the specialized external part, the *cone*, and the internal attenuated *cell-body* occupying the external nuclear layer.

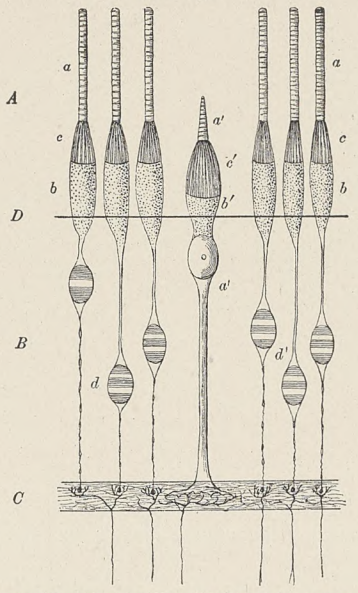
Each *cone* consists of an outer and an inner segment, which, however, differ from the corresponding parts of the rods in the marked inequality of their length, as well as of their diameters. While the outer segment of the rod is almost as long and wide as the inner segment, that of the cone, as usually observed, forms only about one-third of the .031 to .036 millimetre representing the entire length of the cone. The outer piece rapidly tapers from its base, about .002 millimetre in diameter, where it joins the inner segment to a blunted point. The outer ends of the cones lie farther removed from the pigment layer, scarcely reaching so far as the middle of the outer rod-segment. The inner cone-segment is likewise shorter than the corresponding division of the rod. The line of juncture ordinarily presented between the outer and inner cone-segments falls within that of the rods.

The outer cone-segment is further distinguished from the similar part of the rod by the absence of the visual purple, although in many of its characteristics—the possession of high refractive properties, pale color,

[1] Flemming: Zellsubstanz, Kern und Zelltheilung, 1882.

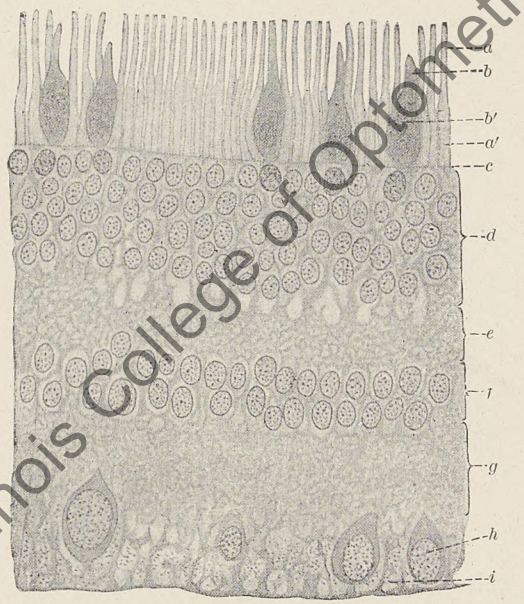
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FIG. 60.



Diagrammatic representation of the visual cells. (Modified from Schultze and Schwalbe.)—*A*, outer portion of visual cells, corresponding to the layer of rods and cones; *B*, inner portion, constituting the outer nuclear layer; *C*, outer plexiform layer in which the visual cells end; *a*, *a'*, outer segments of rods and cones; *b*, *b'*, inner segments of rods and cones; *c*, *c'*, the rod- and cone-ellipsoids; *D*, external limiting membrane, internal to which lie the attenuated bodies of the visual cells represented by the nucleated rod- and cone-fibres (*d*, *d'*), which end in the outer plexiform layer in relation with the arborizations of the bipolar nerve-cells.

FIG. 61.



Section of human retina. (Böhm and v. Davidoff.)—*a*, *a'*, outer and inner segments of rods; *b*, *b'*, outer and inner segments of cones; *c*, membrana limitans externa; *d*, outer nuclear layer; *e*, outer plexiform layer; *f*, inner nuclear layer; *g*, inner plexiform layer; *h*, layer of ganglion-cells; *i*, fibre layer. Magnified 700 diameters.

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keratine envelope, and tendency to split up into disks—it closely resembles the outer segment of the rods.

The inner segment, or body of the cone, presents a notable increase in diameter over all other parts of both cones and rods, being ellipsoidal rather than conical in profile, with a diameter of about .0065 millimetre at the point of greatest swelling. The length of the inner cone-segment is between .022 and .024 millimetre. The outer two-thirds of this segment are appropriated by an ellipsoidal structure which presents a delicate longitudinal striation similar to that found in the inner segment of the rods.

The *body of the cone-visual cell* lies within the outer nuclear layer, and, like that of the rod-cell, consists of the slender cone-fibre and the cone-granule.

The *cone-fibre*, the attenuated protoplasmic column of the neuro-epithelial cell, extends the entire thickness of the outer nuclear stratum and ends within the external zone of the adjoining reticular layer in an expanded base or foot. The fibre is by no means of uniform diameter, but begins next the limitans externa with a width about equal to that of the adjoining portion of the cone of which it is the direct continuation. The most expanded part of the fibre, about .005 millimetre in diameter, is always next the cone, and contains the conspicuous nucleus or cone-granule; the wider portion of the fibre, including approximately the outer third of the entire length, beyond the nucleus rapidly tapers to a slender stalk, which maintains a uniform diameter of about .0012 millimetre throughout the remaining depth of the zone until it reaches the subjacent reticular layer, in the outer part of which it terminates in an expanded base, from which numerous minute processes are given off which stand in close relation with the arborizations of the nerve-cells. Hosch[1] expresses the belief that the relation between the fibrils proceeding from the base of the cone-cells and the processes of the nerve-cells is more intimate than mere apposition, since he finds in the Golgi preparations evidences of direct anatomical continuity between these elements.

The cone-granules, or nuclei of the cone-visual cells, contribute to the characteristic appearance of the outer nuclear layer, but to a less degree than the rod-cells, owing to the numerical preponderance of the latter. The nuclei of the cone-cells occupy the enlarged outer end of the fibre, and consequently are limited to a zone immediately subjacent to the external limiting membrane. This strongly contrasts with the disposition of the rod-nuclei, which are distributed throughout various levels of the outer nuclear stratum. The cone-granules are larger than the nuclei of the rod-cells, possess well-marked nucleoli, but do not exhibit the cross-stripes seen in the corresponding part of the rod-elements.

Peculiar modifications of the cone-cells are sometimes observed in which

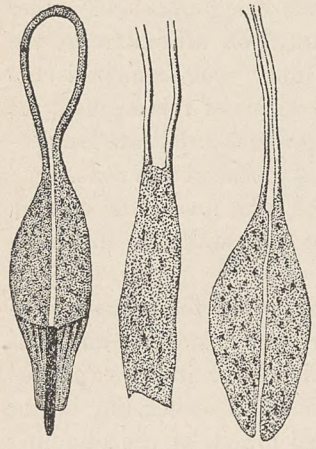
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[1] Hosch: Bau der Säugethiernetzhaut nach Silberpräparaten, Archiv f. Ophthalmol., Bd. XLI. 1895.

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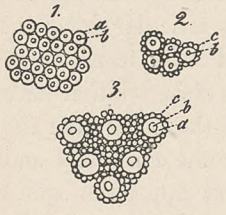
two of these elements are connected, producing the double or "twin cones" first described by Hannover.[1] The more usual form of union is fusion of the bases or inner segments, but Hannover,[2] Pacini,[3] Borysiekiewicz,[4] and Norris and Wallace[5] have described looped connections between the outer segments, the observations of the last-named authors being made upon the human retina. Norris,[6] in a recent communication, accepts the view that "the external extremities of the cones and rods are loops, the outer member of a cone bending over to become continuous with the outer member of an adjacent rod, or less frequently with the outer member of another cone (twin cones). Adjacent rods unite also by their curved outer segments, ending thus also in peripheral loops. . . . The outer member of a cone, having thus curved on itself, runs down along the side of the inner segment as a cylinder having about the same calibre as at the turn, and, after perforating the external limiting membrane, passes alongside of the nucleus at the base of the cone, and may be followed for some distance in a tortuous course between the nuclei of the so-called outer nuclear layer, anastomosing, at times, with some of the other nerve-fibrils of this layer."

FIG. 62.



Diagrammatic view of twin cones. (Hannover.)

FIG. 63.



Surface view of retina, showing disposition and relative number of the rods and cones. (Kölliker.) —1, from the fovea—only cones; 2, from the margin of the macula lutea; 3, from midway between the fovea and the ora serrata; *a*, profile of larger inner segment; *b*, of smaller outer segment; *c*, rod.

The numerical ratio between the rod- and cone-visual cells varies in different portions of the retina. On examining the surface of the retina about midway between its anterior margin and the posterior pole, the field is seen to be studded with closely placed smaller and larger circles which represent the rods and cones seen from their outer extremity. The larger circles contain smaller figures, which are the foreshortenings of the outer cone-segments, the surrounding outline being caused by the greater diameter of the inner part of the cone.

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[1] Hannover: Recherches microscopiques sur le système nerveux, 1844.

[2] Hannover: La rétine de l'homme et des vertébrés, Copenhague, 1876.

[3] Pacini: Nuove ricerche sulla tessitura intima della retina, 1845.

[4] Borysiekiewicz: Untersuchungen über den feineren Bau der Netzhaut, 1887.

[5] Norris and Wallace: A Contribution to the Anatomy of the Human Retina, with a Special Consideration of the Terminal Loops of the Rods and the Cones, University Medical Magazine, vol. VI., March, 1894.

[6] Norris: The Terminal Loops of the Cones and Rods of the Human Retina, Transactions of the American Ophthalmological Society, 1895.

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The cones are separated from one another by a space including three or four rods, this relation, however, becoming markedly changed in the vicinity of the macula. In the latter region the number of cones is so materially increased that immediately outside the macula the cones are separated by only a single row of rods; within the macula the preponderance of the cones is marked to such an extent that the rods are practically wanting, the cone-cells alone being present at the point of greatest visual acuity. While this anatomical detail warrants regarding the cone-cells as the more important factor in the percipient layer in man and other mammals possessing a similar arrangement in the area of sharpest vision, the fact that in some of the lower types, as in the frog, the rods greatly preponderate cautions against assuming that the cone-cells are invariably the more essential structures in the perceptive apparatus. Additional evidence as to the importance of the cones is supplied by the fact that the number of the cones rapidly diminishes towards the ora serrata, at which point they are almost entirely wanting, the well-established low acuity of vision of this portion of the retina agreeing with the numerical paucity of the cones.

The total number of cone-cells contained within the human retina at birth has been placed by Salzer[1] at 3,360,000. The cones in the adult retina have been estimated by Krause[2] at 7,000,000, of which 13,000 are included within the non-vascular area of the macula. (Becker.[3]) The estimates of both Salzer and Krause place the number of cone-cells at about seven times the number of the fibres of the optic nerve. The entire number of rod-cells present in the adult human retina is undoubtedly many times that of the rod-elements. Krause has placed such estimate as high as 130,000,000 rods.

The modifications in the form and arrangement of the visual cells within the macula lutea and at the ora serrata will be considered later with the descriptions of these specialized portions of the retina.

The External Plexiform or Outer Reticular Layer.—This zone represents the first of the strata which collectively constitute the cerebral portion of the retina. As seen in usual preparations, this stratum appears as a narrow, finely granular zone about .010 millimetre in width; when examined with high powers, the granular matrix is resolvable into a delicate reticulum. The true nature of the reticulation of this layer, however, is apparent only after the successful application of the improved methods of staining the processes of nerve-cells.

Recent investigations based upon the results of the Golgi silver and the methylene-blue stainings have shown that the outer reticular layer, in addition to the extremely delicate framework of sustentacular tissue, is made up

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[1] Salzer: Ueber die Anzahl der Sehnervenfasern und der Retinazapfen im Auge des Menschen, Sitzungsberich. der Wiener Akademie, Bd. LXXXI., Abth. iii., 1880.

[2] Krause: Handbuch der menschlichen Anatomie, Bd. II., 1879.

[3] Becker: Die Gefässe der menschlichen Macula lutea, Archiv f. Ophthalmol., Bd. XXVII., 1881.

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of the terminations of the visual cells, the processes and arborizations proceeding from the bipolar nerve-cells situated within the inner nuclear layer, and from the "horizontal cells" belonging to the outer reticular stratum itself.

The exact relation between the central ends of the visual cells and the terminations of the nerve-fibres has long been a subject of investigation and speculation. The observations of Tartuferi, Dogiel, Cajal, and others have demonstrated beyond question the mode of ending of the visual cells within the external plexiform layer. As already noted, the cone-elements terminate within this layer by an expanded coniform base or "foot," while the slender rod-elements end in smaller knob-like thickenings which usually occupy the outermost zone of the reticular stratum. These free endings of the rod-fibres were undoubtedly seen by Max Schultze,[1] as evidenced by his classic delineations of the retina, and also recognized by Hannover,[2] although their full significance, as now appreciated, was not recognized.

Within the inner nuclear layer, composed principally of the bipolar nerve-cells, lie certain elements which are destined particularly for relation with the rod-elements, others especially for the cone-cells. These "rod" and "cone" bipolar cells send off processes into the outer plexiform layer which break up into rich arborizations of terminal filaments immediately beneath the corresponding visual elements and surround the latter with a close ramification of fibrils.

Cajal, Retzius, and those accepting their teaching regard the undoubtedly close relations between these terminal filaments and the bases of the visual cells as limited to intimate juxtaposition and contact, and deny the existence of any direct anatomical continuity between the percipient and the nervous elements. Dogiel, Waldeyer, and Merkel are less ready to accept the doctrine of contact alone, and admit a possible continuity between the delicate threads proceeding from the bases of the visual cells and the processes of the nerve-cells. The weight of evidence, not only from retinal preparations, but also from the conditions obtaining in other neuro-epithelia, leads the author to accept the independent termination of the visual cells, without anatomical continuity, as the true relation between the percipient elements and the nervous processes.

In addition to the intricate reticulation produced by the ascending processes and terminal ramifications of the bipolar nerve-cells, the presence of the "horizontal cells" and their extensions still further conduces to the complexity of the arrangement of fibrils.

The *horizontal*, *basal*, or *stellate cells* have a wide distribution within mammalian retinæ, their presence having been demonstrated by Merkel[3]

[1] Schultze: Zur Anatomie und Physiologie der Retina, Archiv f. mik. Anat., Bd. II., 1866.

[2] Hannover: La retina de l'homme et des vertébrés, 1876.

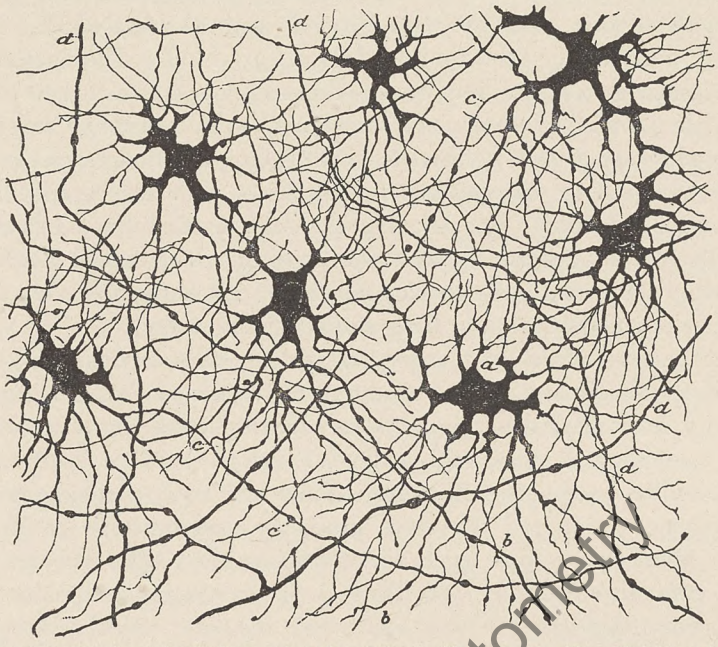
[3] Merkel: Ueber die menschlichen Retina, Archiv f. Ophthalmol., Bd. XX.

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and Kölliker [1] in the calf, Golgi and Manfredi [2] and Rivolta [3] in the horse, Schwalbe [4] and Dogiel [5] in man, and others, including Krause,[6] Tartuferi,[7] and Cajal.[8]

The horizontal cells exist within the outer plexiform layer as two kinds, the *smaller outer* and the *large inner* cells. The *outer horizontal cells* appear as stellate, flattened elements, which occupy the outermost zone of

FIG. 64.



Surface view of horizontal cells from retina of ox stained with methylene-blue. (Cajal.)—*a*, intensely stained cell-body; *b*, richly branched dendrits; *c*, axis-cylinder process; *d*, *d*, scattered axis-cylinder processes undergoing repeated branching.

the plexiform layer and possess a variable diameter, some being as small as .012 millimetre, others as large as .040 millimetre. These elements must be regarded as nerve-cells which take part in the "indirect conduction," since they are provided with both branched protoplasmic and long axis-cylinder processes which extend for considerable distances within the plexiform

[1] Kölliker: Handbuch der Gewebelehre, 5te Aufl., 1867.

[2] Golgi and Manfredi: Annotazioni istologiche sulla retina del cavallo, Accad. di med. di Torino, 1872.

[3] Rivolta: Delle cellule multipolari che formano lo strato intergranuloso o intermedio nella retina del cavallo, Giorn. di Anat., Fisiol. e Patholog. degli Animali, anno III., 1871.

[4] Schwalbe: Handbuch d. ges. Augenheilk., Graefe und Saemisch, Bd. I., 1874.

[5] Dogiel: Ueber die Retina des Menschen, Internat. Monatsschr. f. Anat. u. Histolog., Bd. I., 1884.

[6] Krause: Handbuch der menschlichen Anatomie, Bd. I., 1876.

[7] Tartuferi: Sull' anatomia della retina, Internat. Monatsschr. f. Anat. u. Physiol., 1887.

[8] Cajal: La rétine des vertébrés, La Cellule, t. IX., 1893.

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layer and end in arborizations surrounding the terminations of the visual cells.

The *inner horizontal cells*, of much larger size than the corresponding outer elements, have been especially studied by Tartuferi, Baquis, Dogiel, and Cajal. Following the description of Cajal,[1] the inner horizontal cells include two varieties of elements, those provided with descending processes and those without descending processes.

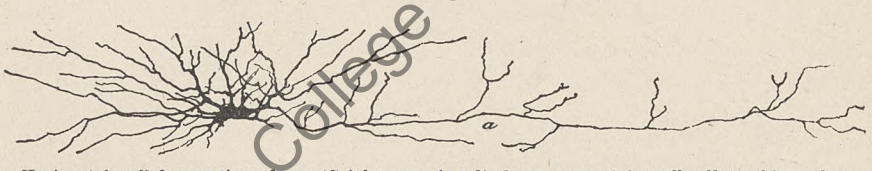
The inner horizontal cells *with descending processes* are large, pyriform or conical in form, with the base directed outward, from which a number of stout, horizontally extending dendrits are given off. These rather short protoplasmic processes rapidly become thinner, irrespective of their division, and, after a limited dichotomous branching, break up into an arborization composed of short varicose threads which end in minute terminal knobs.

The descending protoplasmic process arises from the centrally directed apex of the cell-body. On reaching the outer half of the internal plexiform layer, it divides usually into two branches, which extend horizontally for some distance and end either by forming a rich horizontal plexus within the inner reticular stratum or by gradually fading away.

The neurit, or axis-cylinder process, of these cells is remarkably robust. Beginning usually as a conical enlargement on the cell-body, it runs in a generally horizontal direction, at some distance from the outer reticular layer, throughout a remarkably extended course, the fibre being traceable sometimes for nearly one millimetre without materially changing its course. The statement of Dogiel that these processes bend centrally eventually to become fibres of the fibre layer is not sustained by Cajal, who denies that they become thus deflected from their horizontal course, and maintains, on the contrary, that they probably end within the outer reticular layer.

The inner horizontal cells *without descending processes* have been most accurately described by Cajal,[2] who regards them as the most common of the inner horizontal elements, being much more frequent than those pos-

FIG. 65.



Horizontal cell from retina of ox. (Cajal.)—*a*, axis-cylinder process giving off collateral branches.

sessing the centrally directed process. This authority recognizes two varieties of these cells,—(*a*) those presenting a spindle-form or crescentic body, but slightly protruding, and having only few horizontal protoplasmic processes, and (*b*) those exhibiting a large volume, with conspic-

[1] Cajal: Die Retina der Wirbelthiere, uebersetzt von R. Greeff, Wiesbaden, 1894.
[2] Cajal: loc. cit., p. 121.

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uous bulging on their lower surface, and giving off a large number of divergent processes.

The axis-cylinder process of these cells is very robust, and stretches horizontally, at some distance from the outer reticular layer, throughout an extended course, the first part of which, however, is not infrequently somewhat curved.

The foregoing description of the elements composing the external plexiform layer has emphasized the fact that by far the greater portion of the delicate reticulum constituting this stratum depends for its formation upon the interlacement of the processes of nervous elements. The vertically coursing fibrils are principally contributed by the bipolar cells of the subjacent zone, together with the similarly coursing processes of the horizontal cells; the horizontally coursing filaments are derived from the extended ramifications of the horizontal cells of the reticular layer itself. While undoubtedly the contributions from the several cells compose the great bulk of this layer, yet the presence of a delicate framework of sustentacular tissue must not be ignored. The latter is represented by the apparently granular substance which occupies the interstices of the fibrillar reticulation, and, while small in amount, corresponds closely with the supporting substance unmistakably present in the better developed inner reticular layer, as shown by Schiefferdecker[1] and Dogiel[2] and emphasized by Merkel.[3]

The Layer of Bipolar Nerve-Cells, or the Inner Nuclear Layer.—In ordinary preparations of the retina this stratum appears similar to the outer nuclear zone, being conspicuous by reason of the large number of deeply staining cells which seemingly form the major part of the entire zone. The layer varies in thickness in different parts of the retina, in the vicinity of the optic entrance measuring about .035 millimetre, near the ora serrata diminishing to about .018 millimetre.

The complex constitution of this layer and the varying character of its cellular elements were early recognized, although the subdivision into an outer zone of nerve-cells, the *ganglion retinæ*, and an inner zone of spongioblasts, as made by W. Müller and accepted by many subsequent authors, as Schwalbe, Krause, and others, must be somewhat modified and supplemented in view of the results of the more recent investigations.

The researches of Tartuferi, Dogiel, and Cajal, already cited, have conclusively shown that the bipolar nerve-cells, the principal elements of the layer, consist of two distinct varieties: 1, bipolars especially related to the terminations of the rod visual cells; 2, bipolars particularly destined for the cone elements.

These may be designated, as suggested by Schäfer,[4] respectively the

[1] Schiefferdecker: Studien zur vergleichenden Histologie der Retina, Archiv f. mik. Anat., Bd. XXVIII., 1886.

[2] Dogiel: Neuroglia der Retina beim Menschen, Archiv f. mik. Anat., Bd. XLI., 1893.

[3] Merkel: Ergebnisse der Anatomie und Entwickelungsgesch., Bd. II., 1893, S. 257.

[4] Schäfer: Quain's Anatomy, vol. III., Pt. 3, 1894, p. 43.

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rod- and the *cone-bipolars.* Both fulfil the purpose of supplying the connecting link between the percipient elements and the large nerve-cells of the ganglion layer in the transmission of the light-impulses, their outer ends being closely related to the rod and the cone visual elements, their central expansions with the large ganglion-cells. The cell-body of each gives off two main processes, an ascending protoplasmic or dendrit and a descending axis-cylinder or neurit. The two varieties of bipolars present in their mode of ramification distinguishing peculiarities which call for brief consideration.

The *rod-bipolars* are robust elements of crescentic or oval form, and send off a variable number of ascending protoplasmic processes which freely branch and collectively present a rich arborization within the outer zone of the external plexiform layer. Here the ascending processes end in minute terminal twigs which closely surround the knobbed enlargements of the rod-fibres which descend from the superimposed outer nuclear layer.

The arborizations of the larger rod-bipolars are of such extent that they embrace the free terminations of from fifteen to twenty rod-fibres; those of the smaller cells are much less expanded, and include the terminations of only three or four rods. As already stated, there seems no sufficient evidence for assuming a direct anatomical continuity, close contact between the expanded rod-fibre and the embracing fibrils being the extent of the intimacy between the neuro-epithelial and the nervous filaments.

The descending axis-cylinder processes of the rod-bipolars are very long, passing entirely through the subjacent inner plexiform layer to reach the large elements of the ganglion-cell layer. Immediately above these latter the processes split up into short twigs, which, after closely ramifying over the ganglion-cells, end in ellipsoidal or spherical varicosities.

The *cone-bipolars*, while occurring at all levels, are more numerous within the deeper zone of the inner nuclear layer. Their ascending protoplasmic processes do not pass as deeply into the outer reticular stratum as do those of the rod-bipolars, but end at the level occupied by the expanded conical bases of the cone-fibres. The mode of termination of these processes contrasts strongly with the vertical arborizations of the rod-bipolars, since the terminal fibres in question assume a horizontal direction, expanding into a rich and extensive arborization composed of delicate fibrils which never are deflected vertically. These ramifications lie beneath the expanded bases of the cone-fibres, from which latter twigs pass that bear close relations to the terminal processes of the bipolar cell.

As pointed out by Cajal,[1] the extent of the area included within the expansions of the arborizations of the cone-bipolars renders it highly probable that the more deeply situated rod-fibres also at times may enjoy intimate contact with the processes derived from the second (cone) variety of bipolar nerve-cells, thus establishing an additional path for the conveyance of the particular light-impulses taken up by the rods.

[1] Cajal: loc. cit.

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Plate I.

The elements of the mammalian retina based on the investigations of Ramon y Cajal by means of the Golgi method of silver staining. (Cajal.)

Fig. 2.—Section of dog's retina.—*a*, *a*, cone-fibres; *b*, *b*, rod-granules and fibres; *c*, *d*, bipolar nerve-cells with erect arborizations destined for the rod-elements; *e*, *e*, bipolar nerve-cells with horizontal arborizations destined for the cone-elements; *f*, giant bipolar with horizontal ramifications; *h*, diffuse amacrine cell the processes of which ramify directly upon the large ganglion-cells; *i*, *i*, ascending axis-cylinder processes; *j*, *j*, centrifugal nerve-fibres; *g*, *g*, special elements whose relations are still uncertain; *n*, one of the large ganglion-cells receiving the ramifications of the rod-bipolars; *m*, *m*, nerve-fibres penetrating the inner plexiform layer.

Fig. 3.—Horizontal cells from dog's retina.—*A*, outer horizontal cell; *B*, inner horizontal cell of moderate size without descending protoplasmic process; *C*, inner horizontal cell of small dimension; *a*, *a*, horizontally coursing axis-cylinder processes.

Fig. 4.—Nerve-cells from retina of ox.—*a*, *a*, bipolars with erect arborization; *b*, bipolar with horizontal arborization for cone-cells; *c*, *d*, *e*, similar bipolars the arborizations of which are distributed more superficially; *f*, bipolar with extensive arborization and irregularly coursing descending process; *g*, *g*, bipolars with very extensive horizontal arborizations; *h*, *h*, ovoid cells situated outside the outer plexiform layer; *i*, *j*, *m*, amacrine cells of the inner plexiform layer lying at and distributed to various levels.

Fig. 5.—Horizontally coursing axis-cylinder process from the outer plexiform layer. —*a*, profile view of the terminal arborization; *b*, axis-cylinder.

Fig. 6.—Another form of terminal arborization of a similar process.

Fig. 7.—Nervous elements of retina of ox, especially various forms of amacrine cells distributed to different planes.—*A*, crescentic amacrine with greatly extended process; *B*, large amacrine with thick, widely extended branches; *C*, peculiar amacrine with very slender processes; *D*, amacrine with radiating processes; *E*, large amacrine distributed to deepest stratum; *F*, small amacrine; *G*, *H*, amacrines destined for deeper part of layer; *a*, small ganglion-cell; *b*, ganglion-cell the processes of which form arborizations at three different levels; *c*, ganglion-cell of limited expansion; *d*, ganglion-cell of moderate size; *e*, large-sized ganglion-cell; *f*, ganglion-cell the richly branched processes of which form arborizations within the deeper as well as the superficial levels of the layer.

Fig. 8.—Amacrine and ganglion cells from dog's retina.—*A*, *B*, *C*, *D*, *E*, *F*, *G*, various forms of amacrine cells distributed to different levels of the inner plexiform layer; *a*, *b*, *d*, *e*, *f*, *g*, *i*, ganglion-cells whose arborizations, of varying form and extent, terminate at different planes.

Fig. 9.—Ganglion-cells from dog's retina.—*a*, *b*, *c*, *d*, *f*, *g*, *h*, *i*, ganglion-cells of various size and form terminating in arborizations which occupy different levels within the inner plexiform layer; *A*, *B*, *C*, nervous elements constituting the so-called "spongioblasts."

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PLATE I.



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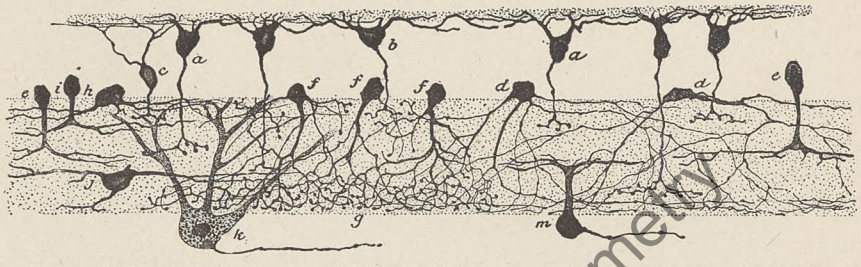
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This same observer has described cone-bipolars of especially large size, —*giant bipolars*,—which usually lie immediately beneath the external plexiform layer. From the large pyramidal or conical bodies of these giant cells processes ascend to form extensive horizontal ramifications within the reticular stratum.

The descending axis-cylinder processes of the cone-bipolars differ markedly in their distribution from the corresponding extensions of the rod-cells. The processes in question, instead of penetrating into the layer of ganglion-cells, are limited to the inner reticular stratum, within which they terminate at definite but various levels. On reaching the particular depth for which it is destined, the process breaks up into fine terminal filaments possessing numerous varicosities: these expansions come into close relation with the arborizations of the ascending processes of some of the large cells situated within the ganglion layer.

The terminations of the cone-bipolars within the inner plexiform layer occur within five definite planes, which arrangement results in the appearances long recognized as the secondary zones of this layer.

FIG. 66.



Nerve-cells from retina of ox stained with methylene-blue. (Cajal.)—*a*, bipolar for cones; *b*, giant bipolar with horizontally expanding processes; *c*, cone-bipolar with deeply situated nucleus; *d*, crescentic cell with delicate, long fibres distributed to the deepest part of the inner plexiform layer; *f*, *f*, *f*, diffuse amacrines forming plexus at *g*; *e*, *h*, *i*, *j*, amacrines; *k*, giant ganglion-cell; *m*, ganglion-cell.

The Amacrine Cells, or Spongioblasts.—W. Müller years ago recognized the fact that the inner nuclear layer contained cells not included with the nervous elements constituting the outer aggregation termed the *ganglion retinæ*. These elements, situated in the deeper zone of the inner reticular layer, Müller regarded as closely concerned in the production of the supporting framework of the stratum, and hence suggested the name of "*spongioblasts*" as appropriate. While the precise nature and relation of these elements are still somewhat uncertain, much has been added to our knowledge of their form and ramifications by the more recent methods of staining. Their peculiarity of apparently being without an axis-cylinder process has led Cajal, by whom they are regarded as nervous elements, to name them the *amacrine cells*, although Dogiel has shown that the homologous structures in the retinæ of amphibia, reptiles, and birds, and possibly also some of the cells in man, undoubtedly possess such processes.

The amacrine cells or spongioblasts of the mammalian retina have been

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studied with great care by Tartuferi, Dogiel, and Cajal. The last-named authority concludes[1] from his investigations that there are present two types of amacrines, the *diffuse* and the *stratiform*.

The *diffuse amacrine cells* occur as large and as small elements. The former possess a triangular, crescentic, or mitral body, from which two or three robust processes obliquely descend, freely branch, and finally form a rich arborization composed of varicose fibrils. These expansions are distributed principally within the lowermost stratum of the inner reticular layer, immediately above the ganglion-cells.

The smaller diffuse amacrines exhibit the same general character as the larger elements; they differ, however, in their oval or "udder-form" body, the smaller number of primary branches, and the position of the terminal twigs, which, while distributed to the inner two-thirds of the plexiform layer, lie within a somewhat higher plane than the endings of the large cells.

The *stratiform amacrine cells*, so designated on account of the manner in which their processes are disposed, are divided by Cajal into three chief groups, although additional subvarieties have been described based upon their relations to the five individual strata of the inner plexiform layer in which the cell-processes end.

While possessing in common descending processes and horizontal ramifications, these cells differ in size, in the robustness of their primary branches, and in the expansion and delicacy of their terminal twigs.

Type I. includes amacrines which possess very large cell-bodies and thick primary stalks; the latter extend into the inner plexiform layer and ramify within one of its sublayers throughout a considerable area. The terminal arborization, however, consists of comparatively few and relatively coarse fibrils.

Type II. comprises smaller amacrines from the medium-sized pyriform body, of which a straight process passes into the inner plexiform layer, where it ends, within one of the substrata, in an arborescence of moderate expansion and close interlacement of the component fibrils.

Type III. is represented by the amacrines of small or medium size giving off a slender process which enters the inner reticular layer and breaks up into a tuft of delicate, horizontally coursing fibrils; these extend radially within one of the substrata and form a terminal arborescence of often very considerable size. In those cases in which the end-fibrillæ are distributed to the outermost zone of the inner plexiform layer, and consequently lie immediately beneath the cell-body of their governing element, the chief process is replaced by a number of small twigs which at once take part in the production of the arborescence.

In addition to the nervous elements contained within the inner nuclear layer, the sustaining neurogliar framework derived from the fibres of

[1] Cajal: loc. cit., p. 134.

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Müller, presently to be described, also contributes a certain number of the nuclei, which become apparent after staining with carmine or hæmatoxylin. These nuclei correspond to the local thickenings of the sustentacular fibres within the inner nuclear layer, and occur at various levels. The supporting framework within this layer consists for the most part of irregular, flattened bands and trabeculæ, which, while imperfectly separating the nerve-cells, suffice to sustain and hold in place the more important elements.

The Internal Plexiform or Inner Reticular Layer.—This stratum in ordinary preparations of the retina is very conspicuous, appearing as a broad, lightly stained zone about .040 millimetre in breadth, which contrasts sharply with the more deeply colored elements of the adjoining inner nuclear and ganglion layers. Seen in such specimens, the stratum apparently is composed of a granular substance, or of a close reticulum of fine fibrillæ, traversed by the long fibres of Müller.

FIG. 67.



Vertical section of retina of ox. (Cajal.)—*a*, *b*, horizontal cells of inner nuclear layer; *c*, *d*, amacrines distributed within inner plexiform layer; *e*, small ganglion-cell; *f–j*, various types of neuroglia cells of the fibre-layer; *k*, interstitial amacrine cell.

While undoubtedly these latter contribute largely to the entire bulk of the layer by means of the delicate reticulum of sustentacular tissue derived from them as lateral processes, it will be seen from the foregoing descriptions of the retinal elements that the terminal ramifications of the processes of the cells contained within the inner nuclear and the ganglion layer form a very considerable proportion of the structures formerly included within the "spongiosum."

As already mentioned, the internal plexiform layer presents a differentiation into five subzones; this specialization depends upon the peculiar manner in which the descending processes of the cone-bipolars and the associated ascending processes of the large ganglion-cells expand at various levels into the horizontal arborescences. The general reticular appearance is still further promoted by the interlacement of the multitude of fibrils derived from the richly branching amacrine cells, one variety of which—the stratiform amacrines—terminates in horizontal ramifications.

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Various authors—H. Müller,[1] Nagel,[2] Borysiekiewicz,[3] and Cajal[4]—have described the presence of small, irregular cells within the inner reticular layer. These elements, the interstitial amacrine cells of Cajal, seem to be displaced cells, whose fusiform or triangular bodies, instead of occupying the usual position within the inner nuclear stratum, have suffered displacement, although their processes terminate in ramifications having the usual destination within the horizontal substrata of the layer. In exceptional cases, however, the distribution of the processes of the displaced cell is thoroughly erratic. According to Cajal, the second substratum is the most frequent location of these aberrant elements. Parallel examples of transposed cells are presented in the unusual positions in which the bipolars and ganglion-cells are found in the retinæ of some of the lower types. It is probable, according to Cajal, that the terminal ramifications of a certain number of "centrifugal" nerve-fibres may still further add to the complex constitution of the internal plexiform layer.

The Layer of Ganglion-Cells.—The especial characteristic of this stratum is, as indicated by its name, the presence of the large, conspicuous nervous elements which are closely related with the fibres composing the optic nerve.

Throughout the greater part of the retina these cells are disposed as a single closely placed row, but towards the visual pole they become more numerous, and in the vicinity of the macula lutea are arranged as a double layer. Within the yellow spot they become greatly increased in number, being superimposed to such an extent that they lie from eight to ten deep. Towards the periphery of the retina, on the contrary, the number of the ganglion-cells decreases, and at the ora serrata they are no longer plentiful enough to constitute a complete row, but lie isolated and widely apart.

The ganglion-cells possess the common characteristics of well-defined multipolar nerve-cells, the neurits or the axis-cylinder processes passing centrally into the nerve-fibres of the fibre layer and optic nerve, and the dendrits or branched protoplasmic processes entering the internal plexiform layer. In their ultimate structure, likewise, the ganglion-cells of the retina correspond with the nervous elements of other parts of the central nervous system. Lenhossék[5] and Dogiel,[6] in their descriptions of the retinal ganglion-cells, recognize the presence of two distinct substances,—a *chromophilous* readily staining and an *achromatic* non-staining material. The disposition of the

[1] H. Müller: Anatomisch-phys. Untersuchungen über die Retina des Menschen und der Wirbelthiere, Zeitschrift f. wiss. Zoologie, Bd. VIII., 1857.

[2] Nagel: Die fettige Degeneration der Netzhaut, Archiv f. Ophthalmol., Bd. VI., 1860.

[3] Borysiekiewicz: Untersuchungen über den feineren Bau der Netzhaut, 1887.

[4] Cajal: Die Retina der Wirbelthiere, 1894, p. 137.

[5] Lenhossék: Der feinere Bau des Nervensystems im Lichte neuester Forschungen, 1895.

[6] Dogiel: Die Structur der Nervenzellen der Retina, Archiv f. mik. Anat., Bd. XLVI., 1895.

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readily tinged constituent of the cell, as demonstrated after staining by Nissl's or Dogiel's modified methylene-blue method, varies greatly, the component granules being arranged singly, grouped, in rows, or as fibrillæ. In opposition to the views of Nissl, Bach,[1] and others, Dogiel supports the older teaching of Max Schultze as to the existence of fibrillation of the nerve-cells, and, further, regards the dendrits and neurits as practically identical in structure. According to the recent investigations of the last-named observer, both protoplasmic and axis-cylinder processes are composed of the same constituents,—namely, chromophilous substance, ground-substance, and fibrillæ,—only in varying quantities. The axis-cylinder process contains only an insignificant amount of the chromophilous and ground-substance, and consists principally of fibrillæ; in the protoplasmic processes, on the contrary, the fibrillæ are inconspicuous, while the staining material and the interstitial matrix are present in much larger quantities.

The more accurate methods of staining now employed reveal differences in the details of the mode of the termination of the dendrits which have led to the recognition of two principal types of the ganglion-cells:

I. Ganglion-cells the protoplasmic processes of which terminate in horizontal ramifications within definite substrata of the inner reticular layer.

II. Ganglion-cells the protoplasmic processes of which end diffusely by ramifications distributed to the entire layer.

The first class further includes two subgroups,—(1) the *monostratified cells*, or those which are distributed to a single substratum of the inner plexiform layer, and (2) the *bistratified* and *multistratified cells*, or those whose processes ramify within two or more substrata.

Each of these subgroups is generally represented by three varieties of cells,—(*a*) *large*, (*b*) *medium*, and (*c*) *small*,—the variation in size being usually included between .03 and .01 millimetre.

Without entering upon a detailed description of the individual elements ramifying within the several substrata, the general character of the three sizes of elements may be noted.

The *large stratified ganglion-cells* give off one, two, or more robust protoplasmic processes which enter the reticular layer and pursue a generally vertical course which varies in length according to the level for which the ramifications are destined. The terminal arborizations extend over a considerable area, are open in arrangement, and come into close relations with the horizontal arborescences formed by the cone-bipolars; the ramifications of a number of the latter are often in relation with the more extended endings of a single ganglion-cell. The neurits or axis-cylinder processes of the ganglion-cells are usually thick, and pass centrally to become the axis-cylinders of the nerve-fibres.

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[1] Bach: Die menschliche Netzhaut in normalen und pathologischen Zuständen, Archiv f. Ophthalmol., Bd. XLI., 1895.

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The *medium-sized stratified ganglion-cells* present considerable variation in their dimensions, but are generally somewhat smaller than the members of the preceding group. The bodies of the elements under consideration are pyriform, the smaller end being directed outward and penetrating for some distance into the inner reticular layer. The terminal arborescences of these cells, composed of closely interwoven varicose filaments of moderate delicacy, are less flattened than those of the other stratified ganglion-cells and include a relatively thick zone.

The *small stratified ganglion-cells* usually possess small pyriform cell-bodies from which a thin, straight, outwardly pointing stalk ascends for a variable distance and ends by breaking up into a terminal arborization of moderate fineness. When the latter is destined for the deepest substratum of the inner plexiform layer, the main stalk may be replaced by numerous delicate processes which undergo but limited division and almost at once take part in the terminal ramifications.

The manner in which the stratified ganglion-cells of the human retina terminate within the substrata of the internal plexiform layer, as shown by the studies of Dogiel by the methylene-blue method, corresponds in essential details with the descriptions of Cajal based upon the use of the Golgi silver stainings.

The *diffuse ganglion-cells* are constant elements of the mammalian retina, although their smaller size and more delicate processes render them inconspicuous in comparison with the giant cells devoted to the horizontal arborizations within the substrata. These elements, as suggested by their name, differ from the foregoing ganglion-cells in the manner in which their peripherally directed dendrits are distributed. Instead of forming arborescences limited to definite substrata, their protoplasmic processes divide into filaments which ramify throughout the plexiform layer, coming, possibly, into close association with the amacrine cells and their ramifications.

The foregoing descriptions have repeatedly emphasized the close relations which exist between the terminal expansions of the bipolars and the ganglion-cells. In the case of the rod-bipolars, the latter alone contribute an arborescence which embraces the upper surface of the ganglion-cell. The expansions of the cone-bipolars, on the contrary, are limited to the inner reticular layer when they are brought into intimate relations with the correspondingly situated expansions of the ganglion-cells.

The nature of the undeniably close relations between these nervous elements has long been the subject of investigation and speculation. The existence of a mutual conjunction within the reticulum formed by the contributions of both has been strictly maintained by many authorities, among whom at the present time Dogiel stands conspicuous. Equally trustworthy authorities, on the other hand, are convinced that net-works of directly continuous filaments do not exist, and that the close contact of the free-ending fibrils composing the terminal arborizations of bipolars and ganglion-

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cells constitutes the limit of the connection between the two and the path for the transmission of light-impulses.

Cajal, in whom the "contact theory" finds one of its stanchest supporters, refers to these relations as follows:[1] "One may well assume that the most limited and most individualized paths of conduction for the light-impulses within the retina always consist of an entire group of bipolars which transfer their impressions to a single ganglion-cell. The terminal ramification of the ganglion-cell is greatly expanded in comparison with the lower arborizations of the bipolars; it is therefore possible that the ramification of a single ganglion-cell comes in contact with a more or less extended group of bipolar cells and receives from them the transmitted light-impulse. The most extensive paths of conduction, consequently, will be afforded by the diffuse or the multistratified ganglion-cells to which is probably transmitted the activity from a large number of bipolars. . . .

"Finally, the object of multiplication of the surfaces of contact, or the horizontal arborizations within the inner plexiform layer, appears to be to render possible a large number of fairly isolated independent paths of conduction within a limited part of the retina. It is evident that were but a single contact stratum present within the inner plexiform layer to receive all the voluminous and extended ramifications contributed by the two factors of the apparatus for nervous conduction (the arborizations of the bipolars and the compressed ramifications of the ganglion-cells), the fairly isolated impulses conveyed from the visual cells would be confused within this stratum to a general impulse, and so the greater part of the distinctness of a perception be lost."

The Layer of Nerve-Fibres.—The vast majority of the nerve-fibres composing this layer of the retina are the continuations of the centrally coursing axis-cylinders of the ganglion-cells above discussed; it is evident, therefore, that the customary manner of speaking of the fibres as passing from the optic nerve to the various retinal areas is a conventionalism, the nerve-fibres really issuing from the ganglion-cells and converging towards the optic entrance in their course to the brain-centres by way of the optic nerve and tract.

The direct continuity between the ganglion-cells and the filaments composing the fibre layer has long been recognized, Corti[2] having pointed out their connection almost half a century ago; the details of the distribution and the relations of the ascending protoplasmic processes of the ganglionic elements, as already described, on the contrary, are among the most recent additions to retinal anatomy.

The nervous filaments of the fibre layer are generally of small or moderate size, but a limited number of very large fibres are also present which have as their presiding elements the ganglion-cells of exceptional size.

[1] Cajal: op. cit., p. 141.

[2] Corti: Beitrag zur Anatomie der Retina, Müller's Archiv, 1850.

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The nerve-fibres arise from the cells as axis-cylinder processes which almost at once assume a horizontal course and become associated with others in coarser or finer bundles. The fibres which possess an unusually large diameter, from .003 to .005 millimetre, generally form groups limited to from four to six axis-cylinders. According to Tartuferi,[1] all the nerve-fibres of the retina exhibit round or oval varicosities distributed at more or less regular intervals along their course, the fibres consisting of the naked axis-cylinders alone; Dogiel,[2] however, regards the varicosities as dependent in a measure both upon the freshness of the tissue examined and upon the size of the fibres, since he has found that in the perfectly fresh retina the varicosities are small and inconspicuous, and, further, that the largest irregularities occur along the axis-cylinders of greatest diameter.

Occasionally the nerve-fibres of the human retina present a variation in the character of their coats, since in some cases the medullary substance, the white matter of Schwann, forms a covering of the axis-cylinders before the fibres have passed through the lamina cribrosa, the usual position at which they obtain their medullary investment. In these rare instances of the premature acquisition of this coat, the so-called "retention of the marrow-sheath," the bundles of medullated fibres become very conspicuous when seen with the ophthalmoscope, appearing as marked white tracts radiating from the optic papilla, in strong contrast to the adjacent parts of the fibre layer retaining their usual transparency. It is of interest to note that in some of the lower animals, as in the rabbit, bundles of medullated fibres are usually present at the lateral margins of the optic disk.

In addition to the centrally coursing fibres, the presence of very fine peripherally directed or "centrifugal" nerve-fibres has been established; these terminate practically within the inner plexiform layer and have no discoverable connection with the cells of the ganglion layer. Cajal[3] has succeeded in demonstrating two varieties of such centrifugal fibres,—those which ascend through the inner plexiform stratum and end in free varicose ramifications in relation with the bodies and descending processes of the amacrine cells, and those which penetrate the plexiform stratum to various levels and then end in horizontal twigs. Regarding the central connections of the centrifugal fibres little is known with certainty beyond their issuing from the fibre layer and assuming a vertical course.

In their ultimate structure the axis-cylinders of the retinal fibres resemble the general composition of the nerve-cells, consisting of deeply staining fibrillæ and an interfibrillar substance which possesses but weak affinity for dyes. The interfibrillar matrix—the *axoplasm* of Schieffer-

[1] Tartuferi: Sull' anatomia della retina, Internat. Monatsschr. f. Anat. u. Physiol., 1887.

[2] Dogiel: Ueber die nervösen Elemente in der Retina des Menschen, Archiv f. mik. Anat., Bd. XL., 1892.

[3] Cajal: loc. cit., p. 143.

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decker[1]—exists in such meagre amount along the ordinary course of the axis-cylinder that the fibrillar structure of the latter is seldom evident in methylene-blue preparations ; at the point of emergence of the axis-cylinder from the ganglion-cell, however, the fibrillation is distinct, owing to the separation of the component threads by the greater quantity of the axoplasm which there exists.

The individual nerve-fibres soon become grouped into bundles, which, while pursuing generally radiating courses having the optic entrance as the common objective point, freely intermingle and form a reticulum.

Assuming, as a matter of convenience, that the optic fibres proceed from the nerve towards the ora serrata in spreading over the retinal area, the disposition of the bundles, as seen in surface views, presents some variation in the two halves of the nervous sheet.

The direction of the nerve-fibre bundles contained within the mesial or nasal half of the retina is strictly radial ; within the lateral or temporal segment, on the other hand, the presence of the macula lutea produces a disturbance of the typical course of the fibres, since the space between the macula and the optic entrance is traversed by from twenty-five to thirty bundles of exceptional delicacy which possess an almost straight path between their point of entrance and the macula, within which they disappear. These groups of fibres which pass between the yellow spot and the optic entrance collectively constitute the *macular bundle* of Michel,[2] by whom the arrangement of the fibres has been carefully studied.

In consequence of the departure from the typical radial arrangement which the delicate macular bundle makes, the adjacent fibres suffer deflection, the upper and lower bundles, after a limited radial course, arching above and below the macular area. Those immediately bounding the macula, after sweeping around the latter in bold curves, unite, while those adjacent, but less closely related, pass beyond the yellow spot and after a time resume their typical radial disposition. Towards the end of their course from the optic entrance to their destination the strands composing the macular bundle become smaller, owing to the deviation of many fibres to take part in the formation of a rich plexus. In the vicinity of the macula the bundles break up into a number of smaller fasciculi ; of the latter, some become resolved into individual nerve-fibres which disappear within the macular area, while others, according to Dogiel,[3] take part in the formation of a ring of fibres which encircles the fovea centralis. Delicate twigs pass from this annular bundle obliquely along the walls of the depression, and, in conjunction with additional fibres from other bundles, form a wide-meshed plexus of nervous fibrillæ which occupies the fundus, as well as the

[1] Schiefferdecker und Kossel: Gewebelehre mit besonderer Berücksichtigung des menschlichen Körpers, Bd. I., p. 200, 1891.

[2] Michel: Ueber die Ausstrahlungsweise der Opticusfasern in der menschlichen Retina, Beiträge zur Anatomie und Physiologie, Festschrift für Ludwig, 1874.

[3] Dogiel: loc. cit., p. 32.

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sides, of the fovea. Dogiel denies that the fibre layer disappears about four-tenths of a millimetre from the foveal centre, as stated by Schwalbe[1] and others, but maintains that it is present within the fundus foveæ as an attenuated layer composed of minute bundles and individual axis-cylinders.

According to this same observer, the arching nerve-bundles which enclose the macula at some little distance from the boundary of the yellow spot, on approaching one another from the opposite sides, break up into small fasciculi or separate fibres which become interwoven to constitute a characteristic net-work. The latter plexus appears as a narrow band, from one to one and a half millimetres in breadth, which begins about one millimetre beyond the outer side of the macula and extends from three to six millimetres to a point where the nerve-bundles resume their usual radial disposition.

The reticulum formed by the bundles of nerve-fibres varies in the size of its meshes in the different parts of the retina, the net-work becoming more open and coarse, the bundles at the same time growing thinner, in the vicinity of the ora serrata, at which point all traces of a fibre layer disappear. On approaching the optic entrance the mesh-work is very dense, and the general thickness of the fibre layer undergoes a corresponding increase.

Since the components of the fibre layer depend upon the ganglion-cells for their origin, a marked inherent variation in the thickness of this stratum in the several portions of the retinal area is to be anticipated from the inequality in the distribution of the ganglion-cells. Where these are numerous and constitute a compact row, as in the vicinity of the posterior pole, the nerve-fibres are likewise present in greater profusion; towards the periphery, on the other hand, where the cells occur with relative infrequency, the fibres are few and the entire thickness of the layer is reduced.

In addition to these inherent differences depending upon the relative number of the nerve-fibres originating within a given area, the progressive accumulation of the fibres as they course towards their common place of exit, the optic papilla, results in a conspicuous increase in the entire thickness of the fibre layer at this place.

At the margin of the optic entrance the fibre layer constitutes more than half the entire thickness of the retina; on leaving this position, however, the stratum rapidly diminishes, so that while at a distance of one-half millimetre it still measures two-tenths of a millimetre, at a point one centimetre farther advanced the layer possesses an insignificant depth. The exceptional thickness at the papillar margin depends not upon superimposed layers of bundles,—an arrangement existing only throughout a limited area above the macula,—but upon the larger size of the individual bundles as they approach their point of exit.

The relation and position of the bundles of nerve-fibres proceeding from the various portions of the retinal field within the optic nerve have elicited

[1] Schwalbe: Lehrbuch der Anatomie der Sinnesorgane, 1887.

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much attention and study. The observations of Gudden,[1] Michel,[2] Ganser,[3] Samelsohn,[4] Schwalbe,[5] and others have shown that the arrangement of the decussating and non-decussating bundles greatly varies among the lower animals; in the latter, as a rule, the crossed fibres predominate, while in man the uncrossed are the more numerous.

The non-decussating bundles of the human retina are derived from the lateral or temporal two-thirds of both retinæ; the crossed fibres largely proceed from the inner or nasal third, but undoubtedly many fibres also are contributed by the outer zones, the temporal two-thirds, therefore, being represented by both crossed and non-decussating bundles.

The macular fibres include both varieties, and occupy a position within the optic nerve near the eyeball, corresponding in transverse sections to a narrow triangular area the apex of which reaches the central vessels and its base the periphery of the optic nerve within the outer and lower quadrant. During their further course towards the chiasm the macular bundle changes its relations, assuming gradually a more central and dorsal position, until within the chiasm they lie collected on the upper surface, close beneath the brain. The well-known case of double central scotoma of the macula, recorded by Vossius,[6] furnished an interesting observation, since the existence of two distinct atrophic areas corresponded to the paths of the crossed and uncrossed bundles, showing that the assumption as to the composite structure of the macular bundle is well founded.

THE RETINAL SUSTENTACULAR TISSUE.

As in other parts of the wall of the neural tube, so also in the retinal area, as represented by the optic vesicles, the elements undergo differentiation into two groups,—the nerve-cells and the closely related neuro-epithelium, and the supporting tissue or neuroglia.

The *neuroglia* or *sustentacular tissue*, a derivative of the ectoderm, is present within the retina in two forms,—(1) as the conspicuous radial fibres of Müller, and (2) as the spider-cells.

The *fibres of Müller* constitute a sustaining framework of considerable complexity which supports the delicate retinal elements and enjoys an intimate relation to all parts of the highly specialized nervous structures. The Müllerian fibres are modified cells which extend through the entire thick-

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[1] Gudden: Ueber die Kreuzung der Nervenfasern im Chiasma nervorum opticorum, Archiv f. Ophthalmol., Bd. xxv., 1879.

[2] Michel: Zur Frage der Sehnervenkreuzung im Chiasma, Archiv f. Ophthalmol., Bd. xxiii., 1877.

[3] Ganser: Ueber die periphere und centrale Anordnung der Sehnervenfasern u. s. w., Archiv f. Psychiatrie, Bd. xiii., 1882.

[4] Samelsohn: Zur Topographie des Faserverlaufes im menschlichen Sehnerven, Med. Centralblatt, No. 23, 1880.

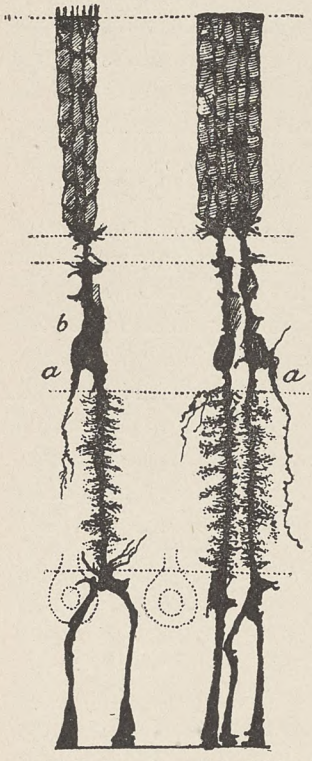
[5] Schwalbe: Lehrbuch der Anatomie der Sinnesorgane, 1887.

[6] Vossius: Ein Fall von beiderseitigem centralem Skotom mit pathologisch-anatomischem Befund, Archiv f. Ophthalmol., Bd. xxviii., 1883.

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ness of the retina, beginning on the inner surface in expanded pyramidal bases and terminating externally in delicate septa which pass between the rods and cones. While in general the fibres constitute slender nucleated columns, their contributions to the support of the elements of the individual retinal layers vary in detail, so that the isolated fibres present a succession of striking differences in various parts of their course.

FIG. 68.



Supporting fibres of Müller, from the peripheral area of retina of ox, after Golgi staining. (Cajal.)—*a*, *a*, descending lateral processes passing from the nucleated enlargement (*b*) within the inner nuclear layer.

The Müllerian fibres become swollen and indistinct after treatment with acetic acid and dilute alkalies. They are not, however, destroyed by boiling in water. The most satisfactory exhibitions of the sustentacular fibres of the retina are had in preparations made by the modified Golgi process or stained by the second of the hæmatoxylin methods suggested by Wolters,[1] those prepared by the last-mentioned procedure being particularly instructive.

The fibres of Müller are found in all parts of the retina, but they are unusually conspicuous in the vicinity of the ora serrata, where they are especially distinct and numerous. Within the macular region, according to Dogiel,[2] they are also very well developed and of exceptional length.

At a level corresponding to the juncture of the rods and cones with the bodies of the visual cells the adjacent sustentacular cells come into apposition and form a seemingly continuous, fenestrated lamella through which the outer segments of the visual cells—the rods and cones—project. This grill-like structure when seen in profile constitutes the apparently continuous *membrana limitans externa*.

The external surface of this horizontally extending perforated lamina is beset with minute vertical processes which lie between the inner segments of the rods and cones and thus probably effect an isolation of the percipient elements.

The expansions of the fibres of Müller within the outer nuclear layer are quite complex in their arrangement. The numerous lateral lamellar

[1] Wolters: Drei neue Methoden zur Mark- und Axencylinderfärbung mittelst Hæmatoxylin, Zeitschrift f. wissensch. Mikroskopie, Bd. VII., 1891.

[2] Dogiel: Neuroglia der Retina des Menschen, Archiv f. mik. Anat., Bd. XLI., 1893.

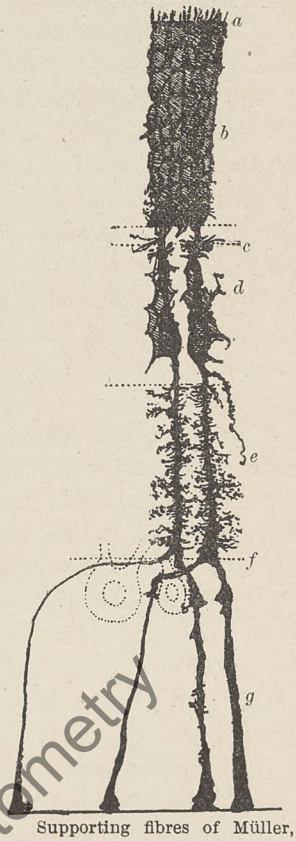
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extensions given off from the fibres break up into secondary plate-like septa and pass between the visual cells, around which they form a close investment, whereby lateral diffusion of the impulses received by these elements is in a great measure prevented. The intricate mesh-work formed by the collateral extensions of this part of the fibre constitutes a striking picture when seen after Golgi staining.

The contributions from the sustentacular fibres to the outer plexiform layer are very inconspicuous, since they consist of lateral projections of such delicacy that they soon become lost amidst the maze of ramifications proceeding from the nerve-cells sending their processes within this stratum. The amount of sustaining tissue within the outer plexiform layer is so inconsiderable that its presence has been overlooked by many authors; there is, however, no doubt that a delicate framework derived from the Müllerian fibres aids in supporting the constitutents of the stratum, a fact emphasized by Schiefferdecker,[1] Merkel,[2] and Dogiel.[3]

Within the inner nuclear layer the sustentacular fibre usually presents its greatest width, its considerable but uncertain thickness being augmented by the presence of a marked local expansion which corresponds to the position of the nucleus of the fibre. The spherical or ellipsoidal nucleus is usually surrounded by an area which suggests the earlier condition of the protoplasm of the fibre before it had so completely lost the characteristics of the primitive cell.

FIG. 69.



Supporting fibres of Müller, from retina of ox, in the vicinity of the papilla, after Golgi staining. (Cajal.) — *a*, processes supporting and isolating the rods and cones; *b*, outer nuclear layer; *c*, outer plexiform layer; *d*, inner nuclear layer, containing the expanded and nucleated portions of the fibres; *e*, inner plexiform layer; *f*, ganglion layer; *g*, nerve-fibre layer, through which the long branched fibres extend.

The lateral expansions of the fibre within this stratum are less extensive than those found within the outer nuclear layer, and, while affording an important means of support for the nervous elements, suffice to form only an incomplete insulation for the bipolars and the amacrine cells which are included within the mesh-work. The enlargement of the fibre corresponding to the position of the nucleus, according

[1] Schiefferdecker: Studien zur vergleichenden Histologie der Retina, Archiv f. mik. Anat., Bd. XXVIII., 1886.

[2] Merkel: Ergebnisse der Anat. u. Entwickelung, Bd. II., 1893, S. 257.

[3] Dogiel: Neuroglia der Retina des Menschen, Archiv f. mik. Anat., Bd. XLI., 1893.

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to Cajal,[1] frequently gives off a descending process of considerable size which passes centrally into the subjacent plexiform layer, within which it terminates after breaking up into a number of endings.

The granular or finely reticular appearance of the inner plexiform layer is largely dependent upon the intricate ramifications of the numberless lateral processes given off from the Müllerian fibres during their course through the stratum. The lateral extensions at once subdivide into delicate fibrils, which pass in a generally horizontal direction and terminate among the arborizations of the nervous elements, to which they contribute material support. In their course they are so disposed that horizontal spaces are continually being left between the bundles of fibrillæ, within which clefts the expansions of the nerve-cells find place. As already noted, the endings of the descending processes given off from the fibres at the nuclear enlargement also contribute to the maze of sustaining tissue within the plexiform stratum.

The ganglion layer receives relatively short, thick, and irregular processes from the compressed Müllerian fibres; these plate-like processes extend between the large nerve-cells of the stratum, which they imperfectly surround and isolate, the ganglion-cells being lodged within niche-like recesses which correspond in size with the dimensions of the nervous element. Within the deeper part of this layer the main column of the fibre frequently divides into two branches, which continue through the fibre layer and end in expanded pyramidal or conical *bases* or *foot-plates*. The bundles of nerve-fibres take advantage of the division of the supporting fibre and pass between the diverging limbs without deflection. Within the fibre layer the sustentacular fibres give off lateral processes in various directions, which, in the form of fibres and plates, join with one another and constitute a series of partitions which separate the bundles of retinal nerve-fibres.

In the vicinity of the optic papilla, when the bundles of nerve-fibres are especially numerous and large, the sustentacular fibres not infrequently divide into three or more limbs, each of which terminates in a conical base or foot.

The expanded bases of the Müllerian fibres lie in close apposition on the inner side of the fibre layer, and, when seen in profile, seemingly constitute a distinct lamella, which has long been described as the *membrana limitans interna*. Surface views of the bases of the sustentacular fibres after silver staining are very striking, the deeply colored lines of cement-substance between the expanded ends of the fibres defining their boundaries with great distinctness and producing a picture strongly recalling endothelium.

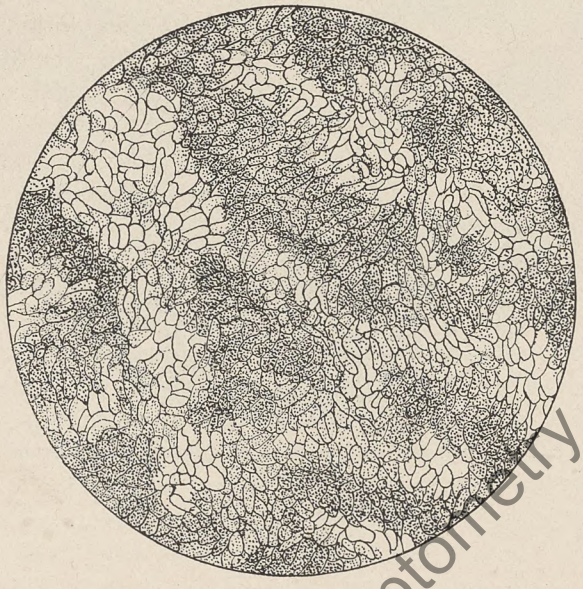
The outlines of the individual bases, as exhibited by the silver lines, are very irregular in both size and form, the figures varying from limited polyhedral areas to large irregular fields. In addition to the usual varia-

[1] Cajal: Die Retina der Wirbelthiere, Wiesbaden, 1894.

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tions in the size and form of the individual fields seen in all parts of the retina, silvered preparations of the peripheral area from the vicinity of the ora serrata demonstrate that the average size of the bases of the fibres within this region is markedly increased, the greater expansion of the base corresponding to the greater prominence of the Müllerian fibres at this point. General diminution of the size of the areas, on the other hand, is very apparent around the optic entrance, the peculiarity depending, probably, upon the more freely branched condition of the fibres in this region and the con-

FIG. 70.



Silver markings of surface of human retina corresponding to bases of fibres of Müller; from a preparation of Professor Norris. Magnified 350 diameters.

sequent smaller size of the individual bases. Conspicuous modifications of the silver picture are presented within the areas corresponding to the course of the larger retinal blood-vessels. As first pointed out by Schelske,[1] and later confirmed by the observations of Schwalbe[2] and of Norris and Shakespeare,[3] the position of the larger vessels may be inferred from the notable modifications in the size and disposition of the bases of the fibres. Over the course of the retinal blood-vessels—both arteries and veins—the basal areas become much narrowed and assume a regular arrangement in which the long dimensions of the fields are disposed at right angles or across the axis of the blood-vessel. On each side of the vessel the usual

[1] Schelske: Ueber die Membrana limitans der menschlichen Netzhaut, Virchow's Archiv, Bd. XXVIII., 1863.

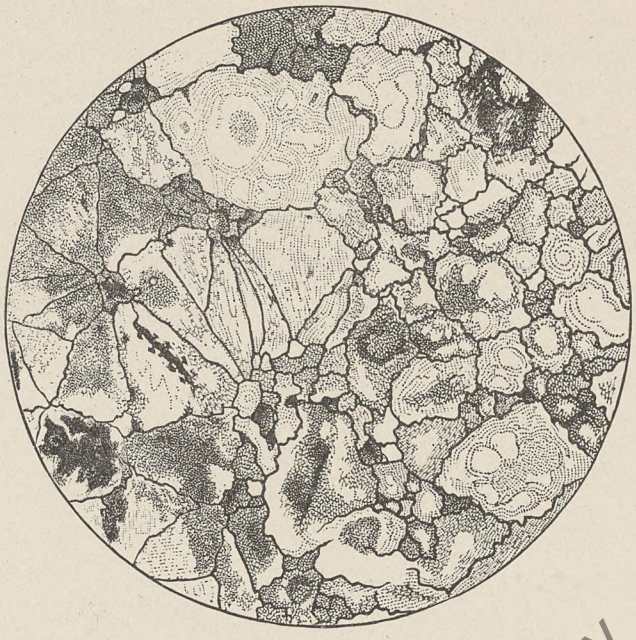
[2] Schwalbe: Die Retina, in Graefe u. Saemisch's Handbuch, Bd. I., 1874, S. 372.

[3] Norris and Shakespeare: A Contribution to the Anatomy of the Human Retina, American Journal of the Medical Sciences, October, 1877.

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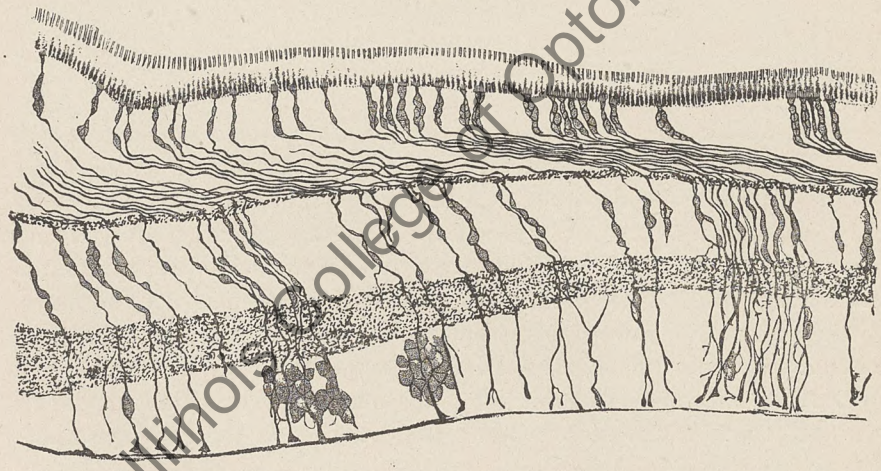
figures abruptly give place to the greatly narrowed areas which extend almost, but not entirely, to the middle of the course of the vessel, the inter-

FIG. 71.



Superficial surface markings from silvered human retina. (Norris and Shakespeare.) Magnified 350 diameters.

FIG. 72.



Section of human retina through the macula, showing the disposition of the fibres of Müller. (Dogiel.)

vening space being occupied by very small additional areas which constitute a band of minute polygonal fields lying over the centre of the vessel. The relation of these less usual figures to the Müllerian fibres is suggested

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in the modified disposition of the bases of the latter at those points where they come into contact with the larger blood-vessels. At such places the fibres diverge to allow the vessel to pass between, their bases undergoing elongation to compensate for the additional area to be covered. Norris and Shakespeare describe a double layer of endothelial markings in surface preparations of silvered human retina; the outer stratum consists of fields very irregular both in size and in form, the inner of much smaller areas, which correspond to the outlines of the bases of the Müllerian fibres.

At variance with the usually accepted opinion that within the macula the sustentacular fibres are rudimentary and without bases, Dogiel[1] and Bach[2] have shown the correctness of the view held by Merkel[3] that the fibres of Müller attain exceptional length and are especially prominent within this area. In retinal preparations after the Golgi method these fibres appear with great distinctness, and are shown to possess the same relations to the several layers of nervous elements, almost as far as the neuro-epithelial stratum, as they do in other parts of the retina, with the single difference that the fibres break up into an unusual number of plate-like septa within the ganglion layers. These partitions present depressions within which the nerve-cells are lodged, the niches varying in size and in form to adapt them to the cells.

On reaching the vicinity of the inner extremities of the cone-cells, however, all sustentacular fibres within the macular area undergo a remarkable and characteristic deflection in their course; the fibres, on arriving at the outer part of the external plexiform layer, bend more or less sharply, sometimes almost at right angles, towards the fovea, and maintain for a variable distance an oblique course towards the visual cells. On attaining the cone-granules, the fibres once more change their direction and reassume their original, generally vertical, course, which they retain as far as the external limiting membrane, giving off numerous plate-like extensions for the reception and support of those portions of the visual cells which constitute the outer nuclear layer at this position. The macular sustentacular fibres, therefore, consist of three portions, an inner and an outer vertical and an intermediate obliquely horizontal segment. The latter is much compressed, and by no means as much laterally expanded as the other parts of the fibre.

In addition to the fibres of Müller, which undoubtedly constitute the important sustaining framework, the existence of *stellate neuroglia-* or *spider-cells* has been demonstrated by the investigations of Borysiekiewicz,[4]

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[1] Dogiel: Neuroglia der Retina des Menschen, Archiv f. mik. Anat., Bd. XLI., 1893.

[2] Bach: Die menschliche Netzhaut nach Untersuchungen mit der Golgi-Cajal'schen Methode, Archiv f. Ophthalmol., Bd. XLI., 1895.

[3] Merkel: Ueber die Macula lutea des Menschen und die Ora Serrata einiger Wirbelthiere, Leipzig, 1870.

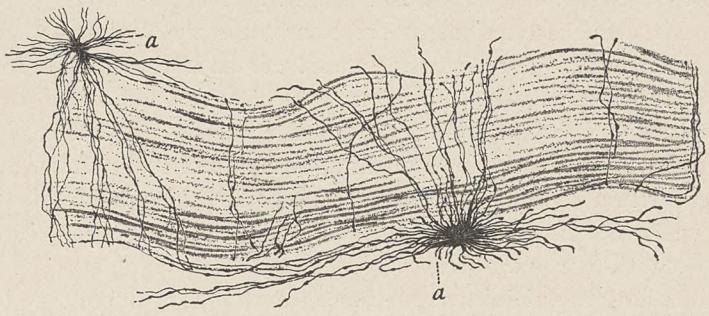
[4] Borysiekiewicz: Untersuchungen über den feineren Bau der Netzhaut, Wien, 1887.

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Cajal,[1] Dogiel,[2] Greeff,[3] and others, although these elements had been imperfectly observed years before by Golgi and Manfredi[4] and by Schwalbe.[5] The spider-cells enjoy but a limited distribution within the retina, being almost entirely confined to the layer of nerve-fibres and its continuation brainward. Bach,[6] however, records their presence within the layer of ganglion-cells. They occur in locations where the fibre layer is best developed, and hence are particularly numerous in the vicinity of the optic entrance.

The neuroglia-cells appear as small stellate bodies, somewhat flattened, and lodged between the bundles of nerve-fibres; their characteristic ap-

FIG. 73.



Portion of bundle of fibre layer of retina in the vicinity of the optic papilla, showing the neuroglia-cells (*a*) after Golgi staining. (Dogiel.)

pearance is due to the large number of delicate fibrillar processes which pass from the cell-body in various directions. These fibrillæ are usually of considerable length and are at first distinctly grouped; the disposition of the flattened cells between the adjacent bundles of nerve-fibres results in the enclosure of the latter by the superficial interfascicular net-works formed by the interwoven processes of the spider-cells. The stellate neuroglia elements occupying the fibre layer of the retina or the optic papilla are surpassed in size by those situated between the nerve-bundles of the optic nerve.

The foregoing description of the retinal layers applies to their disposition as found throughout the greater part of the nervous tunic: two regions, however, require particular consideration, on account of the important modifications which the layers undergo in these particular localities; these specialized areas are the macula lutea, with its contained fovea centralis, and the ora serrata.

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[1] Cajal: Die Retina der Wirbelthiere, Wiesbaden, 1894, S. 145.

[2] Dogiel: Neuroglia der Retina des Menschen, Archiv f. mik. Anat., Bd. XLI., 1893.

[3] Greeff: Die Morphologie und Physiologie der Spinnenzellen im Chiasma, Sehnerv und in der Retina, Verhandlungen der physiolog. Gesellschaft zu Berlin, 1894.

[4] Golgi and Manfredi: Annotazioni istologiche sulla retina del cavallo, Accad. di med. di Torino, 9 Agosto, 1872.

[5] Schwalbe: Die Retina, Graefe und Saemisch's Handbuch, Bd. I. 18.

[6] Bach: Die menschliche Netzhaut nach Untersuchungen mit der Golgi-Cajal'schen Methode, Archiv f. Ophthalmol., Bd. XLI., 1895.

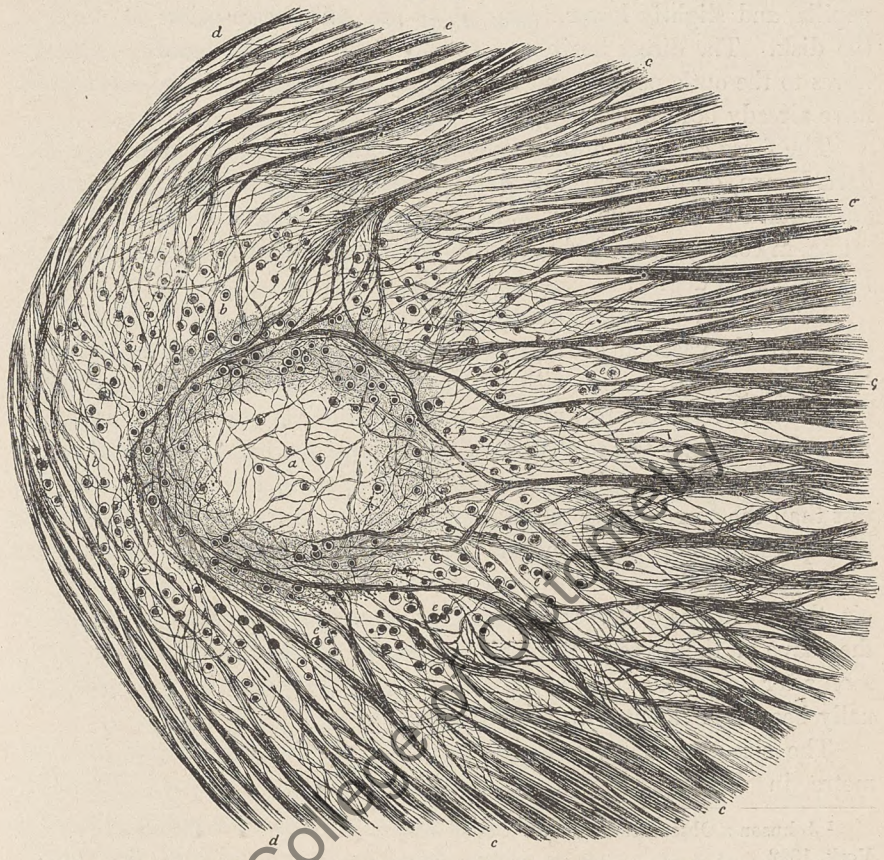
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THE MACULA LUTEA.

As already noted, the immediate vicinity of the posterior pole of the visual axis is marked by a specialized retinal area, the *macula lutea*, or the *yellow spot*, which surrounds the limited *fovea centralis*, in which the visual rays produce their most accurate impressions.

The macula, as observed after death, when the retina no longer possesses the transparency of the living tissue, appears as a distinctly pigmented area,

FIG. 74.



Surface view of macular area of human retina. (Dogiel.)—*a*, fovea centralis, containing a wide-meshed plexus of nerve-fibres; *b*, macula lutea; *c*, macular bundle; *d*, arched marginal bundles sending nerve-fibres to macula; *e*, nerve-cells.

the pronounced yellowish tint of which depends upon the presence of diffuse coloring-matter between the retinal elements within the plane of the visual cells, the latter, however, being devoid of color.

The outline of the macular area is almost circular, rather than elliptical as usually described, the oval form so often attributed to the yellow spot depending more upon ophthalmoscopic appearances than upon anatomical

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examination. Johnson,[1] however, insists that when properly observed the macula appears during life as circular. The investigations of Schmidt-Rimpler,[2] as well as the drawings of Merkel[3] and Dogiel,[4] sustain the approximately circular form of the macula. The greatest diameter of the yellow spot measures about two millimetres, and often does not correspond accurately with the horizontal axis of the eye, making with the latter an angle of from ten to fifteen degrees.

The position of the yellow spot in relation to the optic-nerve entrance is such that the macula lies approximately three millimetres external—three and nine-tenths millimetres, according to Landolt[5]—to the centre of the papilla, and slightly lower, being about one millimetre below the level of the disk. The direct horizontal course of the macular bundles of nerve-fibres to the optic papilla, and the arching disposition of the adjacent fibres, have already been noted.

The *fovea centralis* appears about the centre of the macular area as a dark-brown, deeply pigmented spot; its deep color is not due to any special pigmentation of its own, but to the exceptional thinness of this part of the retina, in consequence of which the superimposed pigment becomes apparent in an unusual degree.

During life, when the beautifully transparent retina allows the presence of the highly vascular choroid to become apparent as the general red reflex of the eye-ground, as seen with the ophthalmoscope, the distinctive color of the macular area is entirely masked, the fovea alone appearing as a brownish-red point. Owing to the absence of rods within the fovea, the visual purple is wanting in this region, which therefore possesses inherently a lighter tint than the surrounding retina, sometimes appearing when examined with the ophthalmoscope as a minute faintly colored spot. The foveal reflex seen with the mirror is due to the direction and slope of the sides of the pit, the variations of the reflex being attributed by Johnson[6] to changes in the shape of the fovea. With the opacity of the retina which supervenes soon after death, the presence of the characteristic yellowish pigment gradually becomes evident within the macula.

The size of the fovea is usually stated as between .2 and .4 millimetre in diameter by various authors, including Kuhnt,[7] Schwalbe,[8]

[1] Johnson: Observations on the Macula Lutea, Archives of Ophthalmology, New York, 1892.

[2] Schmidt-Rimpler: Die Macula lutea anatomisch und ophthalmoscopisch, Archiv f. Ophthalmol., Bd. XXI., 1875.

[3] Merkel: Handbuch der topograph. Anatomie, Bd. I., 1887.

[4] Dogiel: Ueber die nervösen Elemente in der Retina des Menschen, Archiv f. mik. Anat., Taf. II., Bd. XL., 1892.

[5] Landolt: Die directe Entfernung zwischen Macula lutea und Nervus opticus, Med. Centralblatt, No. 45, 1871.

[6] Johnson: loc. cit.

[7] Kuhnt: Ueber den Bau der Fovea centralis des Menschen, Sitzungsber. d. ophthalmol. Gesellsch. in Heidelberg, 1881.

[8] Schwalbe: Anatomie der Sinnesorgane, 1887, S. 89.

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Schäfer,[1] and others, these measurements having been given by H. Müller[2] forty years ago, and even before him by Michaelis.[3] The later investigations, however, of Dimmer,[4] and still more recently of Golding-Bird and Schäfer,[5] show that the accepted foveal diameters are too small, since the fovea measures at least 1.1 millimetres, and may approach, according to Dimmer, in exceptional cases almost two millimetres in its greatest diameter.

The conspicuous modifications of the retinal structure within the macula and the fovea have claimed the attention of the foremost histologists from the days of Heinrich Müller to the present, among those who have particularly studied this region and, in most cases, supplied drawings of the fovea being Henle, Hulke, Merkel, Max Schultze, Krause, Kuhnt, Schwalbe, and Cadiat. While the descriptions of the macular area given by these various authors differ materially as to details, yet all agree in recognizing that the fundamental changes consist in a marked increase in the number of some of the retinal elements within the macula, followed by a rapid thinning out of all, and the final disappearance of certain of the retinal layers within the foveal depression.

In the immediate vicinity of the macula the ganglion-cells are so numerous that they constitute a layer from two to three cells deep; on passing into the yellow spot their number becomes rapidly augmented, until where best developed the ganglion layer contains from six to eight rows of nerve-cells and constitutes a stratum about .07 millimetre in thickness.

The changes affecting the individual layers of the retina within the fovea have been carefully studied anew by Golding-Bird and Schäfer, to whom we are indebted for additional accurate information concerning the details of the disposition and relation of the retinal elements within this area.

On reaching the margin of the circular foveal depression, the greatly thickened ganglion layer rapidly diminishes towards the centre of the basin-shaped pit, the cells becoming less closely packed and much fewer in number until they no longer form a distinct zone, and, finally, at a point corresponding to about one-third of the foveal radius from the centre they are no longer present. The ganglion-cells within the fovea are round or pyriform, and measure about .014 millimetre in diameter; their peripheral processes are directed almost perpendicularly outward towards the inner plexiform layer, within which they probably end in arborizations.

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[1] Schäfer: The Eye, Quain's Anatomy, 10th ed., vol. III., Pt. 3, 1894.

[2] H. Müller: Anatom.-physiol. Untersuchungen über die Retina des Menschen und der Wirbelthiere, Zeitschrift f. wissensch. Zoologie, 1856.

[3] Michaelis: Ueber die Retina, besonders über die Macula lutea und des Foramen centrale, Verhandl. d. Kais. Leop.-Carolin. Acad. d. Naturforscher, Bd. XIX., 1842.

[4] Dimmer: Die ophthalmoskopischen Lichtreflex der Netzhaut, Wien, 1892.

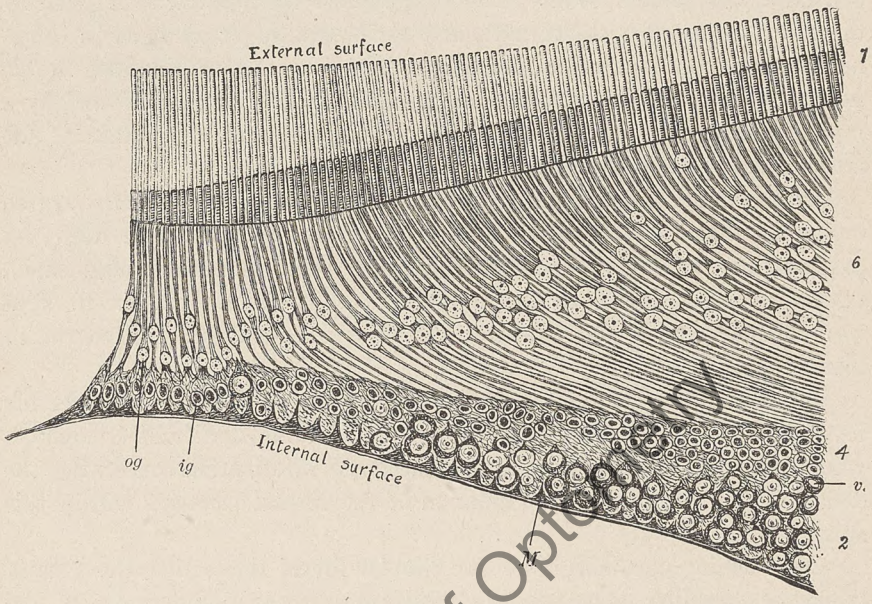
[5] Golding-Bird and Schäfer: Observations on the Structures of the Central Fovea of the Human Eye, Internationale Monatsschrift für Anatomie und Physiologie, Bd. XII., Heft 1, 1895.

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The fibre layer is evidently profoundly affected by the modifications within the stratum of ganglion-cells with which its axis-cylinders are directly continuous. In consequence of these changes the stratum of nerve-fibres very early becomes diminished, and at the edge of the fovea measures only about .015 millimetre in thickness, as a continuous layer entirely disappearing within the fovea where the ganglion-cells cease. According to Dogiel,[1] a few isolated bundles of nerve-fibres cross the fovea and constitute a wide-meshed plexus. (Fig. 75.)

The bipolar nerve-cells, representing the inner nuclear layer, while diminishing greatly in numbers as they approach the floor of the fovea,

FIG. 75.



Diagrammatic section of the human fovea. Magnified 375 diameters. (Golding-Bird and Schäfer.)—2, ganglion layer; 4, inner nuclear layer; 6, outer nuclear layer, the cone-fibres forming the so-called external fibrous layer of Henle; 7, cones; *v*, section of a blood-vessel; *M*, membrana limitans externa; *og*, *ig*, outer and inner granules (cone-nuclei and bipolars) at the centre.

nevertheless continue to the centre of the pit, being there present as an irregular row of small elements embedded within a finely reticular stratum which occupies the space between the membrana limitans interna and the layer of visual cells. This stratum probably represents the fused vestiges of the outer and inner plexiform layers. In the recognition of the bipolars within the centre of the fovea, Golding-Bird and Schäfer deviate from the usual descriptions of this area, although the section of fovea figured by Cadiat suggests the presence of these elements. The combined thickness of the plexiform layers and the bipolars is about .022 millimetre at the bottom of the fovea.

[1] Dogiel: Ueber die nervösen Elemente der Retina des Menschen, Archiv f. mik. Anat., Bd. XL., 1892.

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The most conspicuous stratum within the foveal area is that formed by the visual cells, which here include cone-elements exclusively. This layer at the margin of the depression possesses a depth of about .145 millimetre; while undergoing a material reduction in its thickness in common with the layers already noted, the stratum of visual cells still maintains a thickness of about .064 millimetre at the centre of the fovea, or almost three times the combined depth of the more internally situated layers.

The cone-cells present a striking modification due to the change of position of the nuclei of the fibres. In contrast to the usual position of the cone-granules, close beneath the external limiting membrane, these bodies gradually recede from their normal situation and sink towards the outer plexiform layer, this change being most conspicuous at the bottom of the fovea, where the cone-nuclei almost directly rest upon the reticular stratum. In consequence of these alterations in the position of the outer granules, the relative proportions of the cone-fibre lying beyond and within the granule are reversed, since the outer part between the granule and the external limiting membrane gradually lengthens at the expense of the inner segment of the fibre until the latter practically disappears, and, as in the centrally situated cone-fibres, the cone-granules become "sessile."

Golding-Bird and Schäfer have also called attention to the difference in the character of the two portions of the cone-fibres belonging to the visual cells within the fovea: while the inner segment consists of an attenuated fibre which passes to the outer plexiform layer, in the foveal centre joining the latter by an expanded somewhat triangular base, the external portion possesses the same diameter and appearance as the inner segment of the cones, the direct continuation of which this part of the cone-fibre really is.

Owing to the great thickness of the layer of visual cells at the foveal margin, the stratum at this point measuring .145 millimetre, and the marked obliquity of their course throughout the outer part of the depression, the cone-fibres form a zone of unusual distinctness to which the name *outer fibrous layer of Henle* has been applied. On approaching the floor of the fovea, the fibres are more vertically disposed, and at the centre they ascend almost perpendicularly, their granules being in close proximity to or even sessile upon the underlying plexiform layer.

The characteristic appearance of the fovea depends largely upon the cupping of the two limiting membranes. The outward deflection of the membrana limitans interna has long been recognized, the *fovea interna* (Schäfer) so formed measuring about 1.1 millimetres in diameter and about .130 millimetre in depth.

The participation of the outer limiting membrane in producing the topography of the foveal area has been less certainly recognized; but according to the observations of Ciaccio[1] and of Golding-Bird and Schäfer,[2]

[1] Ciaccio: Notizia sulla forma della fovea centrale ch' è nella macchia lutea della retina umana, Rendic. dell' accad. delle scienze dell' istituto di Bologna, 1880.

[2] Golding-Bird and Schäfer: loc. cit.

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as well as the drawings of Schultze[1] and of Cadiat,[2] a distinct cupping of the membrana limitans externa takes place opposite the depression on the inner surface. A number of authors, on the other hand, including Hulke,[3] Merkel,[4] Henle,[5] Kuhnt,[6] and Schwalbe,[7] describe the outer limiting membrane as passing over the foveal area without cupping. The outer depression, the *fovea externa* (Schäfer), while well marked, is less extensive than the inner pit, measuring about .8 millimetre; its depth, however, equals that of the fovea interna, being about .130 millimetre. Since the layer of cones does not sufficiently compensate by increased thickness for the depression of the outer fovea, it is probable that the pigment layer also dips inward at this point; the individual pigmented elements of this stratum are smaller, but somewhat thickened. The increased space resulting from the inward deflection of the pigment layer is occupied by the local thickening of the choroid, which, as shown by Nuël,[8] takes place opposite the fovea in consequence of the unusual accumulation of capillary blood-vessels which minister to the nutrition of the special retinal area.

The layer of cones presents interesting modifications in the size of its component elements and in its depth: beginning at the foveal margin with a thickness of about .04 millimetre, the stratum gradually increases until at the centre of the fovea externa it measures about .09 millimetre. The cones also exhibit changes, becoming greatly attenuated at the centre, the diameter of the inner segment being only about .0021 millimetre; the length of the inner segment, however, is markedly less than at the margin of the fovea or over the rest of the macula, and contributes only about one-third of the entire length of the cone at the centre of depression. The diameter of the outer cone-segment very closely approximates that of the inner, measuring about .0020 millimetre.

The retinal layers represented at the centre of the fovea, therefore, in addition to the well-developed sustentacular fibres and their expansions, the limiting membranes, are the cone visual cells, constituting the layer of cones and the outer nuclear, here called the external fibrous layer, and the fused outer and inner plexiform layers with the included bipolar nerve-cells. The centrally coursing processes of the last-named elements extend horizontally to end in relation with the ganglion-cells which lie farther towards the periphery of the fovea. The optic fibres do not extend beyond the

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[1] M. Schultze: Die Retina, Stricker's Handbuch, 1872.

[2] Cadiat: Traité d'anatomie générale, t. II., 1881, p. 479.

[3] Hulke: On the Anatomy of the Fovea Centralis of the Human Retina, Philosoph. Transactions, vol. CLVII., 1867.

[4] Merkel: Ueber die Macula lutea des Menschen, Leipzig, 1870.

[5] Henle: Handbuch der Anatomie des Menschen, Bd. II., 1873, S. 690.

[6] Kuhnt: Ueber den Bau der Fovea centralis des Menschen, Sitzungsber. d. ophthalmolog. Gesellsch. in Heidelberg, 1881.

[7] Schwalbe: Anatomie der Sinnesorgane, 1887, S. 110.

[8] Nuël: De la vascularisation de la choroïde et de la nutrition de la rétina principalement au niveau de la fovea centralis, Archives d'ophthalmol., t. XII., 1892.

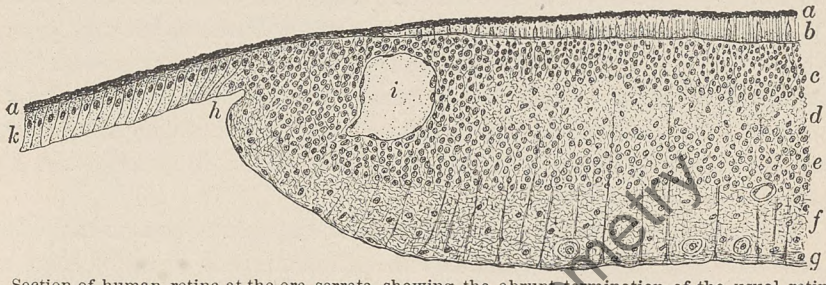
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position of the presiding ganglion-cells, and hence, together with the latter, as a distinct layer, are absent in the fovea centralis.

THE ORA SERRATA.

The ora serrata, marking as it does the extreme peripheral limit of the visual portion of the retina, is distinguished by the abrupt diminution and disappearance of the highly specialized structures concerned in the perception of the light-stimuli, the pigment layer alone of all the retinal strata maintaining its integrity. The regular diminution in the thickness of the retina proceeds gradually from the fundus towards the periphery, so that at this point the nervous coat measures but about one-third of its width at the posterior pole of the eyeball; on reaching the ora serrata, the termination of so many layers within a limited zone only .1 millimetre in breadth results in an abrupt still further reduction, so that the continuation of the retina beyond the ora serrata, as the pars ciliaris, possesses a thickness of only from .04 to .05 millimetre.

FIG. 76.



Section of human retina at the ora serrata, showing the abrupt termination of the usual retinal layers and the continuation of the retinal sheet as the pars ciliaris—*a*, pigment layer; *b*, rods and cones; *c*, outer nuclear layer; *d*, outer plexiform; *e*, inner nuclear; *f*, inner plexiform; *g*, ganglion-cells; *h*, point of transition into inner stratum (*k*) of pars ciliaris; *i*, section of cyst. Magnified 165 diameters.

The sudden decrease in the retinal thickness depends especially upon the rapid reduction and termination of the plexiform layers, the strata of nerve-fibres and ganglion-cells having faded away before reaching the limits of the ora. The layer of rods and cones earliest loses its integrity as a distinct stratum, the rods first disappearing, while the remaining scattered and irregularly disposed cones, imperfectly formed and lacking outer segments, are continued somewhat farther. Of the plexiform strata, the outer earliest disappears, in consequence of which obliteration the fusion of the outer and inner nuclear layers takes place. The inner nuclear layer, of all the constituents of the nervous portion of the retina, is continued farthest forward, usually losing its characteristic appearance near the anterior margin of the ora, where it seemingly passes into the single-celled layer of columnar elements which, together with the external stratum continued from the pigment zone, constitute the layer of the pars ciliaris retinæ.

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The supporting radial fibres of Müller are unusually conspicuous within the ora serrata, since they are here exceptionally well developed and numerous. The round or oval openings, often of considerable size, which are not infrequently encountered near the periphery of the retina, or within the ora, are probably to be referred, as pointed out by Kuhnt,[1] Blessig,[2] and others, to senile changes, since it is doubtful whether such cysts occur in perfectly normal tissue.

The rudimentary anterior retinal segment includes the *pars ciliaris* and the *pars iridica*, both of which are composed of a double layer of cells representing the atrophic layers of the optic vesicle.

The *outer lamina* consists of the pigmented elements continued from the corresponding layer of the posterior segment of the retina. The cells, however, are lower and devoid of the irregular processes which, in the visual area, extend between the outer segments of the rods and cones.

The *inner lamina* consists of the single row of columnar cells, the finely granular or faintly striated protoplasm of which in the ciliary segment is devoid of pigment particles, while in the iridial segment, on the contrary, it is densely crowded with pigment. In the immediate vicinity of the ora their height is from .040 to .050 millimetre, but this gradually becomes reduced to .015 millimetre over the ciliary processes. The additional variations which the elements of this layer present in their transformation from the low columnar type over the ciliary zone to the dark fusiform cells covering the iris have been more fully described in connection with the latter structure.

The exact relation of the inner lamina of the pars ciliaris to the retinal layers has been variously estimated, the columnar cells being by some regarded as the continuation of the inner nuclear layer, by others as the representatives of modified fibres of Müller. Their true nature, however, is indicated by their development; these cells must be regarded, as maintained by Schwalbe, as the continuation of no one particular layer, but rather as independent indifferent elements which have always retained the character of undifferentiated formative retinal elements composing the innermost layer of the optic vesicle.

The delicate glassy membrane, the *limitans ciliaris*, already described as covering the internal surface of the inner cells, is not homologous with the limitans interna of the visual segment of the retina, since it is neither a continuation of this structure nor a product of the specialization of the primary retinal elements, as are the radiating fibres of Müller. The irregular projections, however, which the limitans ciliaris sends into the clefts between the bases of the cylindrical cells suggest, at first sight, a closer relation between the two structures than really exists. The simi-

[1] Kuhnt: Ueber ein neues Endothelhäutchen im Auge, Bericht über die 12. Versammll. der Ophthalm. Gesellschaft in Heidelberg, 1879.

[2] Blessig: De retinæ textura disquisitiones microscopicæ, Dorpat, 1885.

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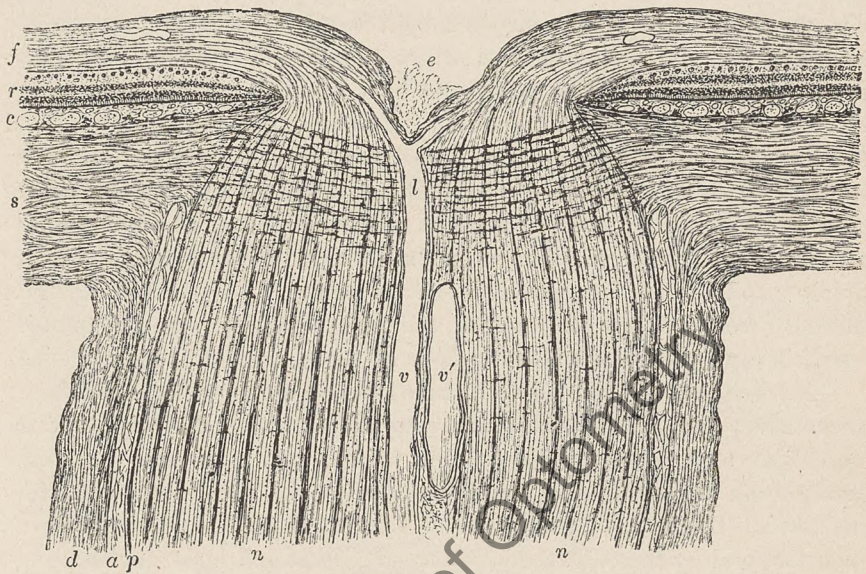
larity of their chemical constituents, as determined by Berger,[1] has also been misleading to those authors who have regarded the cuticular covering of the pars ciliaris and iridica as homologous with the supporting fibres of Müller.

THE OPTIC PAPILLA.

In addition to the two regions characterized by marked modifications in the retinal layers, already considered,—the macula lutea and the ora serrata,—the position of the optic nerve presents a third area of variation.

The *optic papilla*, or *optic entrance*, as it is very generally called, indicates the place towards which the centrally directed axis-cylinders of the fibre layer converge to form the optic nerve and escape from the interior

FIG. 77.



Section of optic entrance.—*n*, *n*, longitudinally cut bundles of optic nerve, surrounded by the dural (*d*), arachnoidal (*a*), and pial (*p*) sheaths; *v*, *v′*, central retinal vessels; *l*, lamina cribrosa; *e*, physiological excavation; *f*, fibre layer of retina (*r*); *c*, choroid; *s*, sclera. Magnified 20 diameters.

of the eyeball in their course towards the cerebral centres. Viewed from the inner surface, as seen with the ophthalmoscope or by inspection of the eye of the recently dead subject, the papilla appears as a circular light-colored area, from one and a half to one and seven-tenths millimetres in diameter, situated about four millimetres to the inner or nasal side and slightly above the posterior pole of the eyeball, as marked by the fovea centralis. The surface of the yellowish-, sometimes bluish-, white optic disk is broken by the main divisions of the central retinal vessels, which emerge from the centre and pass over the periphery of the papilla to gain the fibre layer of the surrounding area.

[1] Berger: Beiträge zur Anatomie der Zonula Zinnii, Archiv f. Ophthalmol., Bd. XXVIII., 1882.

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Viewed in section, the margin of the disk appears slightly higher than the adjacent retina, hence the appropriate name "papilla:" this projection depends upon the unusual thickness of the converging bundles of nerve-fibres, which, as they approach their point of exit, arch over the abruptly interrupted remaining retinal layers and assume their places as the parallel bundles taking part in the formation of the optic nerve. In consequence of the rapid arching of the fibres, as well as of the entrance of the retinal blood-vessels, the central portion of the optic disk is usually occupied by a funnel-shaped depression known as the *physiological excavation*, in contradistinction to that produced by pathological processes.

The position of the physiological excavation usually is central, the depression occupying sometimes as much as two-thirds of the entire papilla, but always leaving a ring of nerve-fibres at the periphery of the disk. The depth of the depression also is subject to much variation; the shallow concavity present in some cases in others is replaced by a deep funnel-like recess, the most dependent point of which may sink to the level of the choroid. The steepness of the walls of the excavation is obviously related to the depth of the depression; the deeper the latter the more perpendicular its sides. In general, the descent of that part of the wall next the macula is more precipitous than in other portions of the excavation, on account of the retinal layers here terminating nearly at the same distance from the centre of the papilla; on the mesial side, on the contrary, they end at different distances from the centre of the disk, the outer layers extending farthest inward, in consequence of which the slope of the excavation is more gradual.

The wedge of retinal tissue included between the arching bundles of nerve-fibres and the choroid which results from the convergence of the fibre layer towards the papilla contains the terminal portions of the retinal layers from the stratum of ganglion-cells to the pigmented epithelium inclusive. The layer of ganglion-cells terminates first, but its cessation is soon followed by that of the succeeding plexiform and inner nuclear zones. The stratum of visual cells, in consequence of its more favorable situation, stretches somewhat farther towards the centre of the papilla, but at the same time presents decided modifications in the disposition of its component parts, the rod and cone and the outer nuclear layer. The most conspicuous of these alterations is the obliquity of the cone- and rod-fibres, the external ends of which are directed inward towards the correspondingly obliquely placed percipient elements, while the internal ends point outward. The outer granules—nuclei of the visual cells—also evince a tendency to recede from their usual situation beneath the limitans externa and to assume instead a position closer to the subjacent plexiform layer; in consequence of this modification the external portion of the cone- and rod-fibres becomes conspicuous as a non-nucleated obliquely striated zone, the *outer fibrous layer* of various authors, which resembles the similarly constituted band within the fovea bearing a like name, and measures about .022 millimetre in thickness.

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Schwalbe[1] has called attention to the existence of a narrow wedge of reticulated tissue which separates the nerve-fibres as they arch into the optic nerve from actual contact with the other retinal layers. This *intermediate tissue*, as named by Kuhnt,[2] is present in somewhat greater amount on the median than on the lateral side, and consists of a reticulum possessing plate-like cells; the tissue apparently is continuous with the framework of the inner retinal layers, being limited externally by the limitans externa. The terminal margin of the choroid marks the external point to which the intermediate tissue extends.

During fœtal life, and sometimes in later years, the excavation of the optic disk is occupied by a peculiar embryonal connective tissue which is closely connected with the central hyaloid artery of the fœtus which it ensheathes. Remains of this structure are often encountered in later years as irregular masses of delicate texture lying within and partially filling the excavation.

FIG. 78.

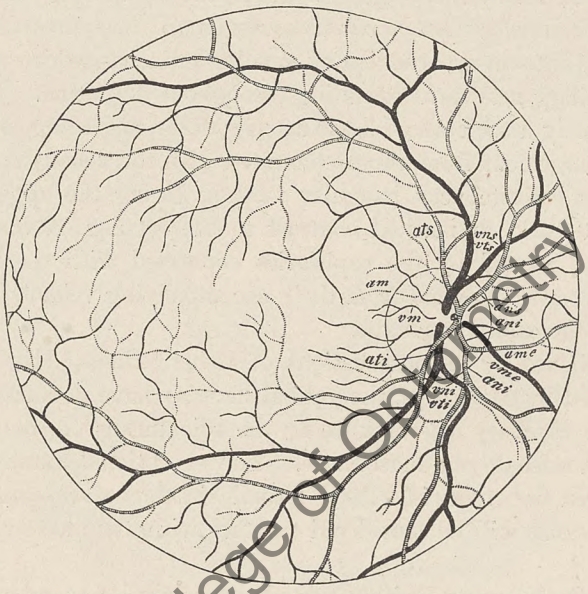


Diagram of the blood-vessels of the human retina. (Leber, after Jaeger.)—*ans*, *vns*, superior nasal artery and vein; *ats*, *vts*, superior temporal artery and vein; *ani*, *vni*, inferior nasal vessels; *ati*, *vti*, inferior temporal vessels; *ame*, *vme*, median vessels; *am*, *vm*, macular vessels.

The Blood-Vessels of the Retina.—The retinal blood-vessels constitute a distinct and closed circulation, of which the *arteria centralis retinæ* and the accompanying vein are the chief stems; in the vicinity of the optic entrance alone does this isolated system communicate with the circulation formed by the ciliary vessels supplying the remaining tunics of the eyeball.

[1] Schwalbe: Der Sehnerv, Graefe u. Saemisch's Handbuch d. Augenheilkunde, Bd. I., 1874.

[2] Kuhnt: Zur Kenntniss des Sehnerven und der Netzhaut, Archiv f. Ophthal., Bd. XXV., 1879.

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At a distance of from fifteen to twenty millimetres from the eyeball, somewhat below and to the outer side, the central artery and vein obliquely penetrate the optic nerve to gain an axial position which is maintained as far as the optic papilla. On reaching the latter position, the central artery divides into two principal stems, the *superior* and *inferior papillary branches*, which are directed respectively almost vertically upward and downward. The papillary branches each subdivide into twigs which pass mesially and laterally and constitute the *arteriæ nasalis et temporalis superior* and *inferior*. Additional small but important direct lateral branches pass outward, as the *arteriæ macularis superior* and *inferior*, for the especial supply of the macular region, these vessels, as noted by Kunn [1] and others, sometimes reaching almost to the fovea centralis, and hence being of moment in aiding in the nutrition of this important area.

After the establishment of the principal stems division rapidly takes place into smaller vessels, which in turn subdivide, but have no communication with one another, belonging to the non-anastomosing "end-arteries." The arterioles have a more tortuous course than the corresponding veins, and break up into an arborization of smaller branches, which terminate in a dense capillary net-work extending throughout the retina. The capillaries immediately associated with the arteries differ, according to Musgrove,[2] in their arrangement from those connected with the venous radicles, since the former constitute very irregular meshes, giving the appearance of a confused net-work, in marked contrast to the regular converging rhomboidal spaces formed by the capillaries connected with the veins. The small arteries are separated from their accompanying veins by an interval occupied by the capillary plexus.

As established by the observations of Leber,[3] Hesse,[4] His,[5] and others, and reaffirmed by Musgrove, the retinal arteries have no anastomotic connections, the capillary net-work being the sole means of communication; the veins likewise do not anastomose. The exceptional connections established between the otherwise closed retinal circulation and that formed by the ciliary vessels will be considered together with the blood-vessels of the optic nerve.

The capillaries expand within two planes, as the *inner* and *outer* vascular plexuses. The exact position of the inner capillary net-work has been a matter of some uncertainty, Hesse, His, and Schwalbe describing it as lying

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[1] Kunn: Ein Fall von Astembolie der Art. centralis retinæ nebst Bemerkungen über d. Verlauf der macularen Arterien, Wiener med. Wochensch., Bd. XLIV., No. 36, 1894.

[2] Musgrove: The Blood-Vessels of the Retina, Journal of Anat. and Physiology, New Series, vol. VI., 1892.

[3] Leber: Die Circulations- und Ernährungsverhältniss des Auges, Graefe u. Saemisch's Handbuch d. Augenheilkunde, Bd. II., 1876.

[4] Hesse: Ueber die Vertheilung der Blutgefässe in der Netzhaut, Archiv f. Anat. u. Physiolog., 1880.

[5] His: Abbildungen über das Gefäss-system der menschlichen Netzhaut und derjenigen des Kaninchens, Archiv f. Anat. u. Physiolog., 1880.

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within the fibre layer, while Musgrove finds it within the ganglion-cell stratum. The sections of human retina examined by the writer show the capillaries to be more numerous within the layer of ganglion-cells than within the fibre zone. The outer capillary plexus lies within the inner nuclear layer, for the nutrition of whose bipolar nerve-cells it is particularly destined. In rare instances the capillaries extend into the outer plexiform zone; never, however, as far as the outer nuclear layer. According to Hesse and His, the inner capillary plexus is distinguished by the coarseness of its meshes; the outer, lying within the inner nuclear layer, possessing close meshes which surround the small ganglion-cells.

FIG. 79.



Accurate drawing of the blood-vessels supplying the macular region of the human retina: from an injected preparation by Heinrich Müller. (Becker.) Magnified 45 diameters.

The retinal veins, beginning in the capillary mesh-works, follow the general course and arrangement of the corresponding arterial vessels quite closely, the venous branches possessing generally a somewhat greater diameter. All the veins and the capillaries are surrounded by delicate adventitious sheaths; between the latter and the wall of the blood-vessel a cleft exists which represents a perivascular lymph-space surrounding the blood-channel.

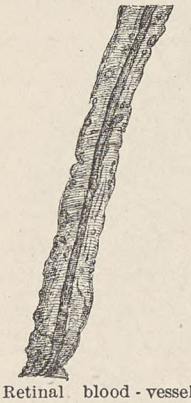
As already noted, the retinal circulation does not penetrate beyond the

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ganglion retinæ, the stratum of visual cells being nourished more especially by the fluids conveyed by the dense capillary net-work within the choroid coat constituting the chorio-capillaris, which lies in close proximity to the outer pigmented cells and the underlying percipient elements.

The fact that the dense net-work of capillary vessels was wanting at the area of the retinal sheet most highly endowed with acute vision has long been established; it has likewise been assumed that the non-vascular area corresponded closely with the fovea, the remaining part of the yellow spot being well supplied with capillaries of the retinal system. The appearance of the paper by Johannides,[1] based upon the examination of the injected retina of a child of four years, in which the presence of blood-vessels within the macula was strongly questioned, called forth contributions to the accurate knowledge of the distribution of the blood-vessels in the communications by Leber,[2] Becker,[3] Gerlach,[4] Reuss,[5] Ayres,[6] and Mayerhausen.[7]

FIG. 80.



Retinal blood-vessel surrounded by perivascular lymph-sheath. Drawn from photograph of preparation of Professor Norris.

These authors agree in regarding the fovea centralis as devoid of retinal blood-vessels, while the remaining part of the macular region is richly supplied. Mayerhausen estimates the surface of the entire macular area at 2.356 square millimetres, of which 2.205 square millimetres are markedly vascular, while the remaining .151 square millimetre represent the non-vascular tract. According to the same observer, the vessels of the macula terminate at .087 to .137 millimetre from the edge of the fovea.

The *lymphatics* of the retina are represented chiefly by the perivascular lymph-channels, already mentioned, which surround the veins and the capillaries and freely communicate with the subpial lymph-spaces of the optic nerve. (Schwalbe.) Additional lymphatic clefts probably exist between the larger nerve-bundles in the vicinity of the papilla. Injections of the subpial space not infrequently also pass between the retina and the pigmented epithelium, as well as between the hyaloid mem-

[1] Johannides: Die gefässlose Stelle der mensch. Retina und deren Verwerthung zur Bestimmung der Ausdehnung der Macula lutea, Archiv f. Ophthalmol., Bd. XXVI., 1880.

[2] Leber: Bemerkung über das Gefäss-system der Netzhaut in der Gegend der Macula lutea, Archiv f. Ophthalmol., Bd. XXVI., 1880.

[3] Becker: Die Gefässe der menschlichen Macula lutea, Archiv f. Ophthalmol., Bd. XXVIII., 1881.

[4] Gerlach: Ueber die Gefässe der Macula lutea, Sitzungsber. der physik.-medicin. Societät zu Erlangen, 1881.

[5] Reuss: Notiz über die Netzhautgefässe im Bereiche der Macula lutea bei Embolia art. cent. ret., Archiv f. Ophthalmol., Bd. XXVII., 1881.

[6] Ayres: Der Blutlauf in der Gegend des gelben Fleckes, Archiv f. Augenheilkunde, Bd. XIII., 1883.

[7] Mayerhausen: Noch einmal der gefässlose Bezirk der menschlichen Retina, Archiv f. Ophthalmol., Bd. XXIX., 1883.

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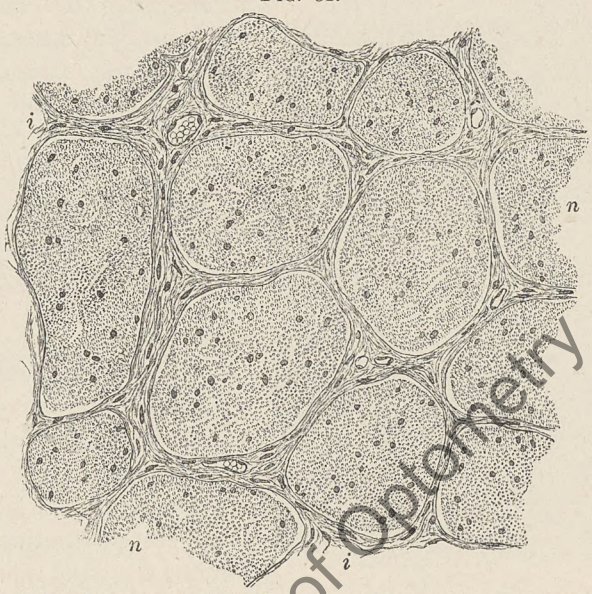
brane and the limitans interna, which extensions of the injection fluid have been regarded by Schwalbe as indicating the presence of lymph-spaces in these positions.

THE OPTIC NERVE.

The optic nerve, owing to the variations in its relations, presents three distinct segments, the *intra-cranial*, the *intra-orbital*, and the *intra-ocular*. The first of these is considered in connection with the optic tract, to which chapter the reader is referred; the description of the remaining parts alone claims attention in this place.

The optic nerve within the orbit, in addition to the obliquity of its course from the optic foramen to the eyeball, presents distinct, although

FIG. 81.



Transverse section of optic nerve.—*n*, *n*, bundles of nerve-fibres separated by vascular septa (*i*, *i*) of connective tissue. Magnified 165 diameters.

inconspicuous, curvatures which render its axis somewhat sigmoid rather than straight. Although, as found by Weiss,[1] great variation in length and curvature undoubtedly exists, yet usually, upon entering the orbit, the nerve bends outward and downward, almost touching the inner surface of the external rectus muscle at the point of greatest deflection; this curve is followed by one less marked in the opposite direction, beyond which the nerve continues straight.

In addition to the foregoing S-like curvature, it is generally assumed, based on the investigations of Vossius,[2] that the optic nerve in the course

[1] Weiss: Anatomie der Eintrittsstelle der Sehnerven, Notiz in Münchner med. Wochenschrift, No. 6, 1889.

[2] Vossius: Beiträge zur Anatomie des Nervus Opticus, Archiv f. Ophthalmol., Bd. XXIX., 1883.

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of its development undergoes a torsion about its longitudinal axis in such manner that the surface which primarily is directed downward closer to the eyeball attains an upward and lateral position and comes to occupy the temporal quadrant. The torsion first appears at a point corresponding to the union of the posterior and middle third of the nerve, and becomes more pronounced towards its anterior extremity. The recent observations of Deyl,[1] however, do not support this view; the last-mentioned author emphatically states that "the described rotation of ninety degrees of the embryonic eyeball does not exist," since the arteria centralis retinæ penetrates the optic nerve always in the median inferior quadrant. This being established, it follows that the assumed inner rotation of the primary fissure does not take place, and, hence, that the suggested close morphological relations of the choroidal fissure and the macula lutea and the fovea centralis must likewise be abandoned.

FIG. 82.



Longitudinal section of optic nerve.—*n*, *n*, bundles of nerve-fibres separated by septa of connective tissue (*i*, *i*). Magnified 165 diameters.

The optic nerve, as seen in transverse sections, consists of about eight hundred distinct bundles of medullated nerve-fibres, separated from one another by connective-tissue trabeculæ and septa which are derived as extensions from the general pial sheath.

The entire nerve corresponds in its structure to a gigantic funiculus, the penetrating pial tissue forming the septa representing the endoneurium and the pial sheath proper the perineurium. The optic nerve, furthermore, must be regarded as part of the central nervous mass, being, according to Monro,[2] comparable to the posterior columns of the spinal cord.

The bundles are composed of medullated nerve-fibres of an average diameter of about .002 millimetre; the extremes of the thickness of the individual fibres, however, include a wide range, many fibres being so fine that their width is inappreciable, while others of less frequency possess a diameter of from .005 to .010 millimetre.

The entire number of nerve-fibres contained within the optic nerve has

[1] Deyl: Ueber den Eintritt der Arteria centralis retinæ in den Sehnerv beim Menschen, Anatom. Anzeiger, Bd. XI., No. 22, 1896.

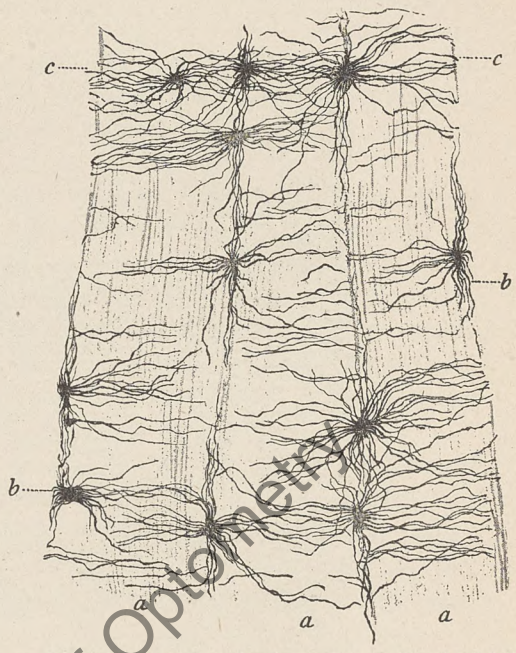
[2] Monro: The Optic Nerve as a Part of the Central Nervous System, Journal of Anatomy and Physiology, N. S., vol. X., 1895.

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been variously stated. The estimates of Salzer[1] and of Krause,[2] in which the number of measurable fibres is placed at about four hundred and twenty-five thousand, may be regarded as approximately correct.

The close relation already noted which exists between the retina and its stalk and the more centrally situated nervous masses is still further emphasized by the correspondence in the structure of the fibres composing the optic nerve and those of the brain and the spinal cord; as are the latter, so are the former devoid of a neurilemma, the medullated axis-cylinders being held in place by the interstitial supporting substance, the neuroglia. Robinson[3] formulates the genetic relations of the optic nerve as follows: "In mammals the optic stalk becomes converted into the optic nerve by the transformation of its protoplasmic substance into retiform sustentacular tissue, and by the passage of nerve-fibres through its walls, the nerve-fibres being protected and supported by the external limiting membrane of the stalk, and by the reticular framework formed by the modification of its walls, the transformation from the stalk to the nerve being associated with the disappearance of the cavity of the stalk." The recent investigations of Dogiel, Cajal, Greeff, and Bach, to which reference has already been made, conclusively show the presence of large neuroglia-cells within the supporting tissue of the optic bundles. These spider-cells, when stained by the Golgi or other improved method, are very conspicuous elements, resembling the similar though smaller bodies found within the fibre layer of the retina. Additional flattened cells lie within the connective tissue separating the nerve-bundles, their deeply stained nuclei contrasting strongly with the feebly colored nervous tissue.

FIG. 83.



Longitudinal section of optic nerve stained by the Golgi method to display the neuroglia-cells. (Dogiel.)—*a*, bundles of nerve-fibres; *b*, neuroglia-cells; *c*, similar cells near the optic papilla.

[1] Salzer: Ueber die Anzahl der Sehnervenfasern und der Retinazapfen im Auge des Menschen, Sitzungsber. der k. Akad. d. Wissensch., Bd. LXXXI., 1880.

[2] Krause: Ueber die Fasern des Sehnerven, Archiv f. Ophthalmol., Bd. XXVI., 1880.

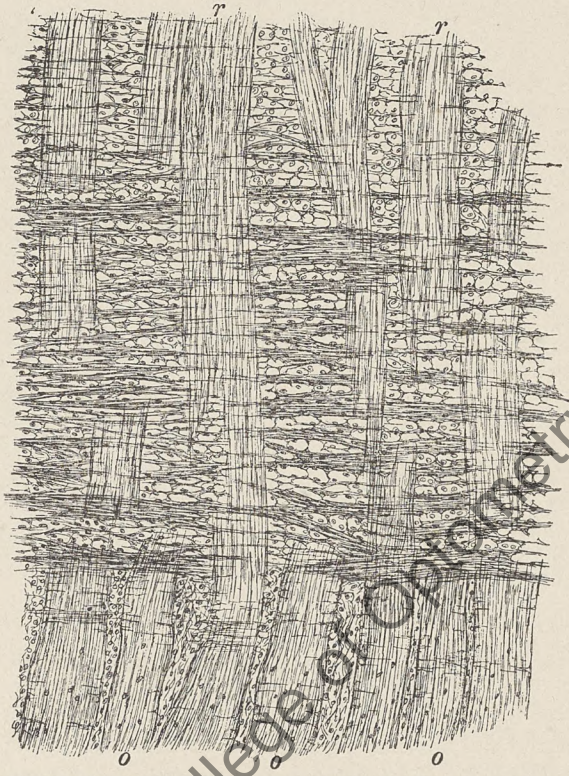
[3] Robinson: Formation and Structure of the Optic Nerve, and its Relation to the Optic Stalk, Journal of Anatomy and Physiology, vol. XXX. 3, 1896.

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On reaching the intra-ocular portion of the optic nerve, the nerve-fibres sooner or later undergo a conspicuous change, since they usually lose the medullary substance in their passage through the lamina cribrosa, or, to state it more accurately, gain the white substance of Schwann on emerging from the cribriform lamella of the sclera in their course from the retina brainward.

In consequence of the disappearance of the medullary coat, as well as of a large part of the interfibrillar supporting tissue, the diameter of the optic nerve becomes rapidly diminished on approaching its retinal expan-

Fig. 84.



Section of the lamina cribrosa showing the passage of the bundles of optic fibres (*o*, *o*) through the felt-work formed by the scleral tissue. — *r*, *r*, bundles of nerve-fibres emerging from the retina. Magnified 165 diameters.

sion; the diameter of about three millimetres which it possesses at the exterior of the ball is reduced to about one and five-tenths millimetres during its passage through the lamina cribrosa. The nerve presents its least diameter within the zone corresponding to the inner fourth of the sclera and the choroid; the relation of the latter coat, however, is variable, since in some cases the choroidal ring marks the most constricted part of the nerve, while in others the optic trunk is distinctly wider at this point than where embraced by the scleral constriction.

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This latter structure consists of a series of several—from four to eight—horizontal interlacements of scleral fibres which extend between the bundles of the optic nerve, as the latter traverses the outer tunic of the eyeball, and collectively constitute the *lamina cribrosa*. The bridging fibres originate mostly within the inner third of the scleral coat, but receive additional support by their close connection with the septa within the optic nerve, particularly with the central mass of connective tissue surrounding the retinal vessels.

The several horizontal mesh-works are supplemented by trabeculæ which extend obliquely or longitudinally and still further unite the individual reticula with one another. The trabeculæ which pass from the scleral tissue towards the centre of the nerve usually support blood-vessels, in consequence of which arrangement the optic nerve, at the base of the papilla, is traversed by a vascular net-work of exceptional richness, whereby the important communication between the ciliary and the retinal vessels is established.

In addition to the scleral bands, delicate trabeculæ from the choroid coat also penetrate among the optic nerve bundles and constitute what has been termed, in accordance with the investigations of Kuhnt[1] and of Hoffmann,[2] the *choroidal portion* of the lamina cribrosa, a part which in early life represents a relatively more important constituent. Delicate extensions of the blood-vessels of the choroid are also converged within these trabeculæ, by means of which the anastomosis between the retinal and choroidal circulations is effected.

Mention has been incidentally made of the communications which exist between the circulation established by the ciliary vessels, including the scleral and choroid plexuses, and that formed by the arteria centralis retinæ. The earliest literature concerning the cilio-retinal anastomosis includes mention of the existence of such communication by Hovius (1716), Zinn (1753), Waller (1754), Tiedemann (1824), and Sömmering (1844); of these, the description of the relations of the ciliary vessels around the optic nerve given by Zinn is the most complete, in recognition of which the vascular wreath encircling the optic nerve has been termed the *circulus arteriosus Zinnii*. Jaeger,[3] however, particularly called attention to the importance of this communication, and supplied additional data concerning its details. Subsequently Leber[4] emphasized this supplementary source of nutrition of the nerve and a limited retinal area, to which Czermak[5] later

[1] Kuhnt: Zur Kenntniss des Sehnerven und der Netzhaut, Archiv f. Ophthalmol., Bd. xxv., 1879.

[2] Hoffmann: Zur vergleichenden Anatomie der Lamina cribrosa nervi optici u. s. w., Archiv f. Ophthalmol., Bd. xxix., 1883.

[3] Jaeger: Ueber die Einstellungen des dioptrischen Apparates im menschlichen Auge, Wien, 1861, Anmerkung, S. 52.

[4] Leber: Bemerkungen über die Circulations-Verhältnisse des Opticus und der Retina, Archiv f. Ophthalmol., Bd. xviii., 1872.

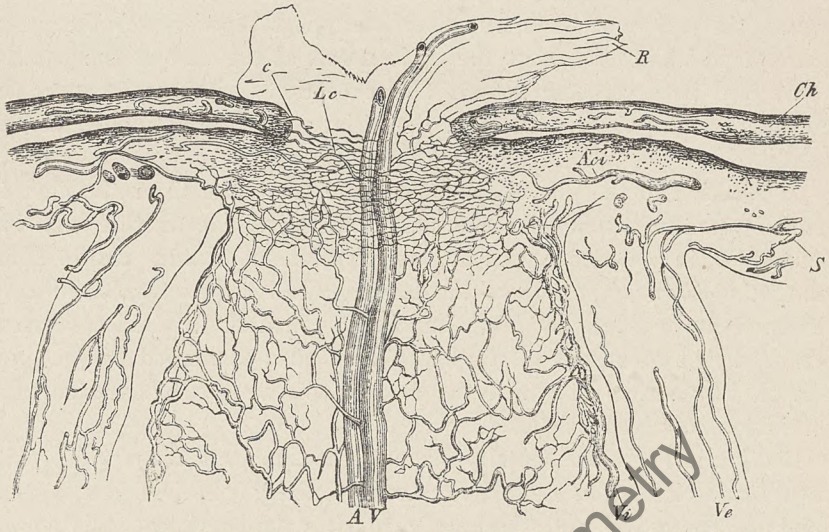
[5] Czermak: Beitrag zur Kenntniss der sogenan. cilio-retinalen Gefässe, Wiener Klinische Wochenschrift, No. 11, 1888.

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added testimony to show that the cilio-retinal vessels supply especially the macular region.

The vascular circuit of Zinn which encircles the optic nerve entrance is formed by branches from the short posterior ciliary arteries; from this vascular wreath robust branches are sent to the choroid, while delicate twigs pass to the lamina cribrosa and indirectly communicate with the central vessels of the retina by means of the intervening capillaries with which both sets of vessels anastomose. Likewise, delicate twigs derived

FIG. 85.



Longitudinal section through the optic entrance showing blood-vessels injected from ophthalmic artery. (Leber.)—*S*, sclera; *Ch*, choroid; *R*, retina; *Ve*, outer, *Vi*, inner optic sheath; *A*, arteria centralis retinæ; *V*, vena centralis retinæ; *Lc*, lamina cribrosa; *Aci*, short post-ciliary arteries, giving off twig to optic nerve; *c*, anastomosis between choroidal and retinal vessels.

from the choroidal plexus penetrate along the trabeculæ constituting the innermost part of the lamina cribrosa and thus effect a capillary union between the central retinal and the choroidal vessels. As an exceptional arrangement larger trunks belonging to the cilio-retinal vessels may pass to the optic head and the retina.

The practical importance of these communications has been emphasized by the clinical and experimental observations of Rumschewitsch,[1] Wagenmann,[2] Adamük,[3] Randall,[4] and others; by these it was shown that after the usual source of blood-supply from the central retinal artery had been

[1] Rumschewitsch: Ueber die Anastomosen der hinteren Ciliargefässe mit denen des Opticus und der Retina, Klinische Monatsblätter f. Augenheilkunde, Bd. XXVII., 1889.

[2] Wagenmann: Experimentelle Untersuchungen über den Einfluss der Circulation in der Netzhaut und Aderhautgefässen u. s. w., Archiv f. Ophthal., Bd. XXXVI., 1890.

[3] Adamük: Zur Frage ueber den Einfluss der Chorioidea auf die Ernährung der Netzhaut, Archiv f. Augenheilkunde, Bd. XXVII., 1893.

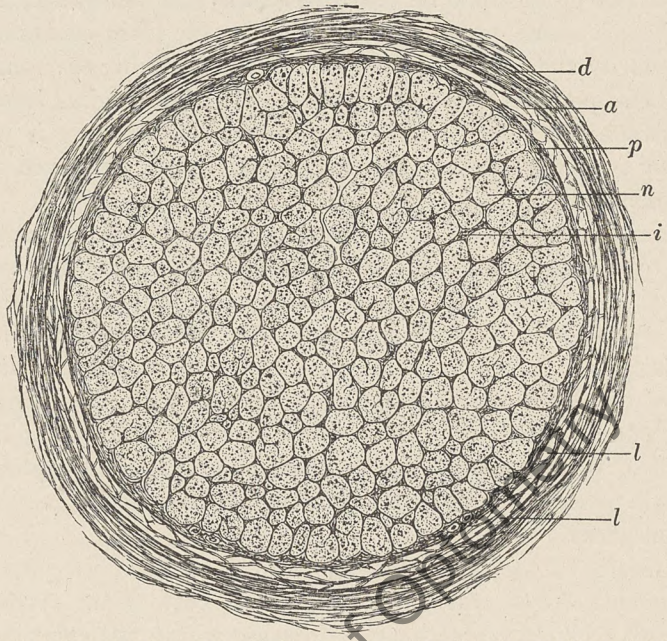
[4] Randall: Cilio-Retinal or Aberrant Vessels, Trans. American Ophthalmol. Society, 1887.

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cut off, either by embolism or by ligation, the collateral circulation established from the choroidal system sufficed to maintain the nutrition of the posterior retinal area.

The explanation of the communications between the retinal and ciliary arteries around the papilla is to be sought in the early distribution of the arteries of this region, since, as pointed out by Eversbusch,[1] the optic head with the lamina cribrosa is supplied, in addition to the central artery, by a dense capillary net-work derived from the sclera and choroid. While the older view, by which the vitreous vessels were credited with an active rôle

FIG. 86.



Transverse section of optic nerve with its sheaths.—*n*, bundle of nerve-fibres; *i*, interfascicular connective tissue; *d*, *a*, *p*, respectively dural, subarachnoidal, and pial sheaths enclosing lymph-spaces, *l*, *l*. Magnified 20 diameters.

in the vascularization of the young retina, is no longer tenable in the light of the careful researches of O. Schultze,[2] who has shown that the retinal vessels develop entirely independently of those of the choroid, the early intimate relations between the retinal vessels and those of the surrounding choroid and sclera persist to a limited degree and are represented by the minute branches of communication found in the adult organ. Exceptionally one of these embryonic vessels undergoes greater development than usual, and then appears as a cilio-retinal branch seen with the ophthalmoscope.

[1] Eversbusch: Klin.-anatom. Beiträge zur Embryologie und Teratologie des Glaskörpers, Mittheilungen d. königl. Univ.-Augenklinik zu München, Bd. I., 1882.

[2] O. Schultze: Zur Entwickelungsgeschichte des Gefass-Systems im Säugetier-Auge, Kölliker's Festschrift, 1892.

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The Sheaths of the Optic Nerve.—The intra-orbital portion of the optic nerve is enveloped by three distinct sheaths, the direct prolongations of the brain-membranes. These envelopes begin at the cranial surface of the optic foramen, where they spring from the meninges, and terminate in the fibrous tunic of the eyeball, with which they blend.

The *outer* or *dural sheath*, the direct continuation of the dura mater of the brain, is a thick fibrous covering which loosely envelops the nerve-trunk within the orbit, but closely embraces it, together with the other sheaths, at the optic foramen. On reaching the eyeball, the dural sheath bends sharply outward and becomes continuous with the outer part of the sclerotic coat.

The surface of the optic nerve is invested by the pial sheath, the extension of the pia mater, which closely resembles the brain-membrane in its rich vascularity and is an essential factor in maintaining the nutrition of the peripheral portions of the nerve-trunk. The intervaginal lymph-space which separates the outer from the inner sheaths of the nerve is unequally divided by a delicate septum, the *arachnoidal sheath*, continued from the central arachnoid.

The arachnoidal sheath is so closely connected with the outer dural covering by means of numerous trabeculæ that only a narrow, irregularly interrupted cleft separates the two sheaths; this interstice constitutes the subdural space, and is continuous with the corresponding intra-cranial lymphatic space. The wider cleft between the arachnoidal and pial sheaths constitutes the *subarachnoidal space*, continuous with the corresponding space surrounding the brain, across which stretch the irregular trabeculæ and bands of the arachnoidal tissue; these, as well as the lymph-spaces of the nerve in general, are more or less perfectly invested by a covering of endothelial plates.

The sheaths of the optic nerve, as well as the included subdural and subarachnoidal spaces, end within the fibrous coat of the eyeball. The dural sheath, as already mentioned, terminates within the outer two-thirds of the sclera by sharply bending over into the fibrous tissue of this coat. The arachnoidal sheath fuses with the dural envelope shortly before ending, the termination of its fibres being traceable into the middle third of the sclera. The greater part of the pial sheath likewise fades away in the sclerotic coat, blending with the inner third; the most internal fibres, however, probably extend still farther and become connected with the choroid. The subdural and subarachnoidal compartments of the intervaginal space likewise terminate within the sclera, the fusion of the arachnoidal and pial sheaths with the fibrous tunic marking the points at which these lymph-spaces respectively end. In exceptional cases, as noted by Michel,[1] the spaces may be somewhat prolonged as clefts which extend parallel to the surfaces of the sclera between its inner and middle thirds.

[1] Michel: Beiträge zur näheren Kenntniss der hinteren Lymphbahnen des Auges, Archiv f. Ophthal., Bd. XVIII., 1872.

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The pial sheath is intimately related to the optic nerve bundles not only at the periphery but throughout the trunk. The pial covering gives off numerous septa which penetrate in all directions within the nerve and subdivide the nervous tissue into the hundreds of bundles of nerve-fibres already noted, thus corresponding to the coarser trabeculæ of the endoneurium of other nerves. At the point where the central retinal blood-vessels abruptly pierce the periphery to gain the interior of the optic nerve, a robust extension of the pial sheath accompanies the vessels and thenceforth occupies the centre of the nerve as the axial perivascular connective tissue.

The blood-vessels supported by the larger pial trabeculæ are of importance in nourishing the nerve-bundles; after the entrance of the central retinal vessels, the minute twigs directly given off from these branches constitute additional sources for the supply of the axial portions of the optic nerve. According to Krause,[1] the pial tissue surrounding the central retinal vessels also contains a delicate nervous plexus which accompanies the blood-vessels.

The *lymphatics* of the optic nerve, in addition to the lymph-spaces within the sheaths already noted, are represented by clefts situated between the nerve-bundles and the intervening pial septa. These channels, as well as the intra-fascicular interstices between the groups of nerve-fibres, communicate, according to Schwalbe,[2] with the intra-vaginal lymphatic tracts.

THE CRYSTALLINE LENS.

The *lens*, or *lens crystallina*, is the most important part of the dioptric system of the eye, since the refractive changes necessary for accommodation are mainly effected by the alterations of its curvatures, and hence of its power of focussing rays upon the retina proceeding from objects situated at various distances.

The lens of the human eye is a transparent biconvex body, with circular outline and rounded margin, which measures about four millimetres in its sagittal and from nine to ten millimetres in its transverse diameter. Seen in profile, the anterior surface is less convex than the posterior, the respective radii of curvature of the two surfaces during accommodation for distant objects being ten millimetres and six millimetres; during accommodation for near objects the lens thickens and its surfaces become distinctly more convex. In this latter condition the radii of curvature increase to six millimetres and five and a half millimetres for the anterior and posterior surfaces respectively; the change, moreover, affects the anterior to a much greater degree than the posterior curvature. When critically examined, the lens curvatures are found not to be quite spherical, Brücke[3]

[1] Krause: Die Nerven der Arteria centralis retinæ u. s. w., Archiv f. Ophthal., Bd. XXI., 1875.

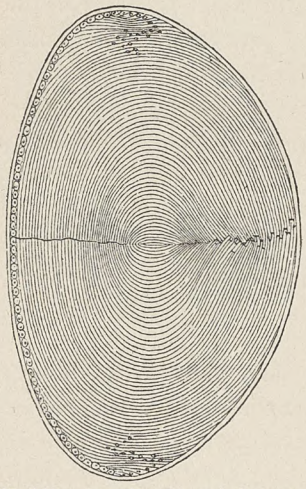
[2] Schwalbe: Ueber Lymphbahnen der Netzhaut und des Glaskörpers, Berichte der königl. sachs. Gesellschaft der Wissensch., 1872.

[3] Brücke: Anatomische Beschreibung des menschlichen Augapfels, 1847.

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having shown long ago that the anterior surface corresponds to the segment of an ellipsoid, the posterior to a paraboloid. The form of the lens also varies at different periods of life. The lens of early childhood is relatively thicker and more convex than that of the adult; old age, on the other hand, is attended by a diminution of the curvatures, the senile lens being distinctly flatter than normal. The fœtal lens approaches the spherical form, and by the end of gestation has attained, according to Sappey[1] and Jaeger,[2] almost its fully developed sagittal diameter. The transverse diameter, on the contrary, is subject to augmentation after birth, since from a measurement of seven millimetres, which it possesses in the new-born, it increases to eight millimetres by the twelfth year, and reaches its full size by about the eighteenth year.

FIG. 87.



Meridional section through human lens. (Babuchin.)

Lying between the iris in front and the vitreous behind, the relations of the lens are such that its anterior surface fills the pupillary opening and supports the pupillary margin of the iris, which rests upon the lens for a variable distance; the peripheral zone of the lens lies behind and separated from the iris by the intervening posterior chamber, to the posterior boundary of which space the anterior lens-surface contributes. The posterior surface of the lens lies within a depression, the patellar fossa, situated in the anterior surface of the vitreous body; its margin is in relation with the ciliary body, to which it is attached by means of the supporting fibres of the suspensory ligament.

The *lens-substance* during life is doubly refracting, perfectly transparent, and colorless, acquiring, however, a light straw tint in advanced age. It exhibits a differentiation into a harder, less elastic core, the *nucleus lentis*, which occupies the centre, and the superficial, softer, compressible peripheral layer, the *substantia corticalis;* the transition from one to the other, however, is very gradual and without distinct demarcation. The contrast between the superficial and deeper layers depends not upon inherent structural differences, but upon the larger amount of tissue-juice contained within the cortex in consequence of its more favorable situation for the imbibition of the nutritive fluids by means of which alone the vitality of the non-vascular lens is maintained.

The nucleus obviously enjoys less opportunity for active nutrition than does the cortex, and in consequence is the part which earliest undergoes changes resulting in the characteristic hardness and, in late life, slight

[1] Sappey: Traité d'anatomie descriptive, 1889, t. III. p. 761.

[2] Jaeger: Ueber die Einstellung des dioptrischen Apparatus im menschlichen Auge, 1861.

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coloration and even opacity observed within the central portion of the lens. The fact that the most recently formed, and hence least resistant, lens-substance lies superficially also must be borne in mind when considering the causes of the softness of the cortex. The refractive index of the lens-substance, as determined by Helmholtz,[1] is from 1.44 to 1.45; according to Krause,[2] the cortex is less highly refracting than the nucleus, the indices of the two being 1.4053 and 1.4541 respectively. The crystalline lens, together with its envelope, presents histologically three structures for consideration,—the *lens-capsule*, the *subcapsular epithelium*, and the *lens-fibres*.

A knowledge of the development of the lens is so essential for an appreciation of the true significance of its structure that a brief recapitulation of the manner of its formation may be here presented with advantage, the reader being referred to the section treating of the Development of the Eye for the details of the somewhat intricate histogenesis.

It will be recalled that the lens develops from an invagination of the ectoderm, which rapidly becomes converted into the closed lens-sac by the approximation and subsequent union of the lips of the epithelial recess. Soon all connection with the surface ectoderm is lost, the lens then being represented by a sac the epithelial walls of which are no longer of uniform thickness, but already present a differentiation into a broader posterior and a thinner anterior layer. The contrast between these layers rapidly becomes more marked as the lens develops, in consequence of the great increase in the growth and length of the cells constituting the posterior wall and their conversion into the lens-fibres. At first of large size, the cavity of the lens-sac gradually becomes reduced by the encroachment of the rapidly thickening posterior wall, until finally it is entirely obliterated by the apposition of the lens-fibres against the cells of the anterior wall, which meanwhile, notwithstanding their slight increase in numbers, retain the character of epithelial elements.

The primary lens-substance, therefore, is the product at first entirely of the growth and differentiation of the elements of the posterior layer of the lens-sac, the anterior cells remaining largely passive. With the increasing dimensions of the lens, however, the original posterior cells no longer suffice, and it becomes necessary to produce new and additional lens-fibres; these augmentations take place at the periphery of the now solid lens by the conversion of the most peripherally situated elements of the anterior layer. This region, the so-called *transitional zone*, henceforth until the completion of the growth of the lens becomes the seat of a constant metamorphosis whereby the short columnar marginal cells of the anterior layer are converted into the meridionally arranged lens-fibres. The elements of

[1] Helmholtz: Ueber die Accommodation des Auges, Archiv f. Ophthalmol., Bd. I., 1855.

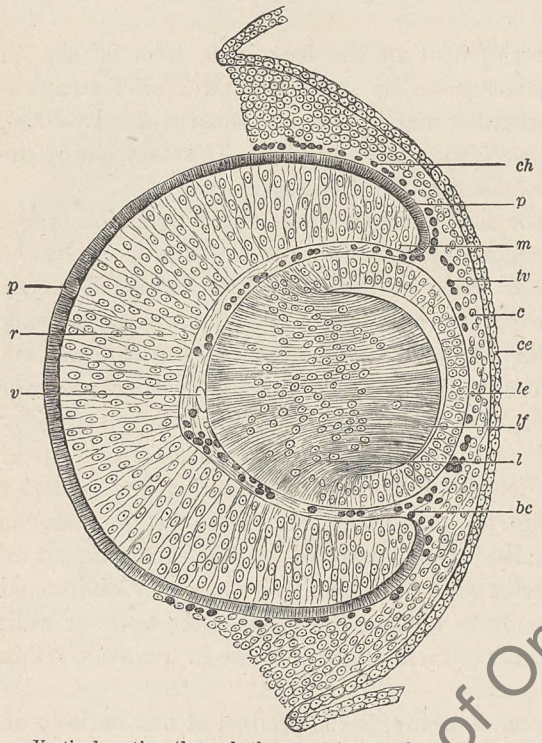
[2] Krause: Die Brechungsindices der durchsichtigen Medien des menschlichen Auges, 1855.

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the anterior stratum which are never needed for the production of lens-fibres persist as a single layer of polygonal, mostly hexagonal, cells situated beneath the capsule, and constitute the epithelium of the anterior capsule, or subcapsular epithelium.

The capsule of the lens is entirely different in origin, being probably largely, if not entirely, the derivative of the mesodermic tissue which at an early period surrounds the primitive lens as an extension of the vitreous mesoderm occupying the cavity of the secondary optic cup. The primitive vitreous tissue immediately surrounding the posterior surface of the lens is highly vascular in consequence of the rich net-work of radially coursing capillaries derived from the breaking up of the hyaloid artery in the vicinity of the posterior pole of the lens. The vascular sheet of vitreous mesoderm thus differentiated constitutes the *membrana capsularis*.

FIG. 88.



Vertical section through the eye, at an early stage, of an embryo mouse. Enlarged 130 times. (After Kessler, from Hertwig's Lehrbuch.)—*p*, pigmented epithelium, forming the outer layer of the secondary optic cup; *r*, thickened inner layer, the future retina; *m*, marginal zone, or border of secondary optic vesicle, which develops later into the non-sensory, ciliary, and iritic portions of the retina (uveal tract); *v*, vitreous body, with blood-vessels; *tv*, tunica vasculosa lentis; *bc*, blood-corpuscles; *ch*, choroid; *lf*, lens-fibres; *le*, anterior epithelium of lens; *l*, nuclear zone of lens-fibres; *c*, connective-tissue layer (corium) of cornea; *ce*, outer corneal epithelium.

At the margin of the lens the capsular membrane passes to the anterior surface of the lens, which it completely covers, though designated by different names. Before reaching the centre of this surface the radially arranged capillaries continued from the posterior net-work are joined by supplementary vessels proceeding from the pupillary margin of the iris; the additional vessels so derived are venous in character and aid in carrying off the blood conveyed by the branches of the hyaloid artery.

The part of the anterior vascular stratum closing the pupillary opening constitutes the *membrana pupillaris*, the remaining portion, occupying the peripheral zone, the *membrana capsulo-pupillaris*. While receiving distinctive names, it must be remembered that the pupillary and capsulo-

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pupillary membranes are really parts of the same vascular mesodermic envelope that constitutes the membrana capsularis.

With the advanced development of the lens, the important services of the vascular capsular membrane in supplying the rapidly growing lens with nourishment terminate, and in the human eye the structure undergoes atrophy and disappearance before birth; as well known, in some mammals, on the contrary, the membrana capsularis persists for a short time after birth, the still conspicuous pupillary membrane of the new-born kitten affording a familiar example.

The foregoing intimate relations between the lens and the surrounding vascular envelope at once suggest a mesodermic origin for the lens-capsule, the only difficulty in accepting such derivation for the latter structure being the fact, as established by the observations of Kölliker,[1] Kessler,[2] and others, that the immediate lens-capsule exists before the appearance of the vascular mesodermic membrana capsularis. This precedence is interpreted by these authorities as indicating that the lens-capsule must be regarded as a cuticular structure formed through the agency of the ectodermic elements of the lens-sac, a view already accepted by H. Müller.[3]

Notwithstanding these observations, the genetic relation of the mesodermic tissue to the capsule seems undeniable, and is accepted by a majority of anatomists, including Zernoff[4] and Waldeyer.[5] A possible twofold origin, from the mesoderm posteriorly and from the ectodermic cells anteriorly, has been suggested by Manz:[6] while this view is untenable, in consideration of the continuity of all parts of the capsule, which undoubtedly possess a common origin, the manifestly close relation of the surrounding mesodermic tissue and the intimate attachment of the suspensory fibres to the somewhat differentiated superficial *zonular lamella* have led Schwalbe[7] to entertain the opinion that possibly the innermost portion of the capsule is a cuticular formation produced by the lens-cells, the external layer of the capsule being a product of the surrounding mesoderm. In view of the variance of opinion, it must be admitted that the derivation of the lens-capsule is still uncertain, and awaits renewed study of developmental stages; the writer, however, from the examination of the developing eyes of rabbit embryos, inclines to the opinion that the entire capsule is of mesodermic origin.

The Capsule of the Lens.—The capsule completely envelops the lens,

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[1] Kölliker: Entwickelungsgeschichte des Menschen und der höheren Thiere, 1879.

[2] Kessler: Zur Entwickelung des Auges der Wirbelthiere, 1877.

[3] H. Müller: Anatomische Beiträge zur Ophthalmologie, Archiv f. Ophthalmol., Bd. II., 1856.

[4] Zernoff: Zur Entwickelung des Auges, Centralblatt f. d. med. Wissenschaft., No. 13, 1872.

[5] Waldeyer: Entwickelungsgeschichte des Auges, Jahresbericht f. Ophthalmol., 1872.

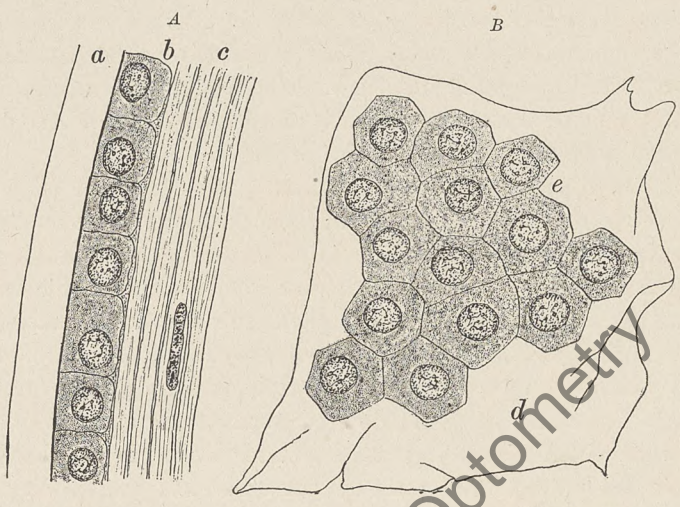
[6] Manz: Entwickelungsgeschichte des menschlichen Auges, Handbuch d. Augenheilkunde, von Graefe u. Saemisch, Bd. II., 1876.

[7] Schwalbe: Lehrbuch der Anatomie der Sinnesorgane, 1887, S. 127.

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and by its intimate attachment with the suspensory fibres proceeding from the ciliary region forms an important part of the supporting apparatus of the lens. It is a transparent, highly elastic membrane, which, while continuous in all parts, is conventionally divided into the anterior and posterior capsule covering the respective surfaces of the lens. The capsule varies in thickness, being considerably stouter in the central area of its anterior segment, where it attains a thickness of from .010 to .015 millimetre, and thinner at the periphery; the most attenuated portion corresponds to the middle of the posterior surface, at which point the membrane is reduced to from .005 to .007 millimetre in thickness. In its chemical composition and reactions the lens-capsule corresponds neither to elastic nor to white

FIG. 89.



A, section of crystalline lens embracing capsule (*a*), anterior epithelium (*b*), and most superficial fibres (*c*) of cortex; *B*, portion of lens-capsule (*d*) seen from the surface, with a number of anterior epithelial cells (*e*) still adherent. Magnified 500 diameters.

fibrous tissue, but approaches most closely to the sarcolemma and the basement membrane of glands.

The histological details of the capsule are negative, the membrane possessing no cells, and at most exhibiting an indication of lamellæ as expressed by a fine parallel striation seen in sections when examined under high magnification. After maceration in a solution of potassium permanganate, Berger[1] succeeded in splitting up the capsule into lamellæ corresponding with the parallel markings seen in section; the separation of the most superficial stratum, the *zonular lamella*, most readily takes place, the more deeply situated portion of the capsule stoutly resisting cleavage. The pronounced tendency to undergo this division is regarded by some authorities, among

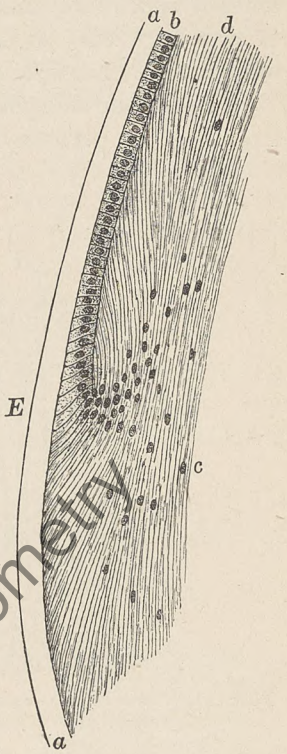
[1] Berger: Bemerkungen über die Linsenkapsel, Centralblatt f. prakt. Augenheilkunde, 1882.

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whom is Schwalbe,[1] as strong evidence in favor of a double origin of the capsule, the outer layer being mesodermic, and the inner derived from the ectoderm as a cuticular formation produced by the epithelium of the lens-sac.

The Epithelium of the Lens.—The epithelium constitutes the most anterior layer of the lens proper, and, as already pointed out, represents the remains of the front wall of the primary lens-sac. It consists of a single layer of polyhedral, mostly six-sided, flattened cells, about .020 millimetre in diameter; in early life the cells are smaller and cuboidal, measuring about .010 millimetre in each dimension. The finely granular protoplasm contains usually a spherical nucleus about .005 millimetre in diameter, often nucleoli, and sometimes vacuoles. The epithelial cells extend with their anterior ends into the thin layer of subcapsular stratum of albuminous material which serves to connect the capsule with the epithelium; the embedded ends of the cells sometimes present irregular projections which give an irregular contour to the epithelial elements.

FIG. 90.



Meridional section through equatorial region of young lens, showing zone of transformation (*E*), in which cells of anterior epithelium (*b*) are converted into lens-fibres (*d*); *c*, nucleated young fibres; *a*, lens-capsule. Magnified 240 diameters.

On approaching the margin of the lens, the epithelial cells, in addition to becoming more granular, undergo important change in form, assuming more and more markedly the columnar type; the columnar cells, in turn, are replaced in the equatorial region by the extended lens-fibres into which they elongate. The elements within the transition-zone at first present a slightly sinuous axis; as the curve becomes more marked, however, its concavity is directed outward. Coincidently with the rapid increase in the length of the transforming cells, their axes gradually become straight and then bowed in the opposite direction, the concavities looking outward. As a result of these variations in the axes of the developing lens-fibres, the marginal portions of the lens in meridional sections present the peculiar appearance which has been termed the *lens-whorl* by O. Becker.[2]

When critically examined, the increase which takes place in the length of the cylindrical cells during their conversion into the lens-fibres is seen to be especially dependent upon the rapid growth of the extra-nuclear half of the cell,—that is, of the part lying between the nucleus and the anterior

[1] Schwalbe: loc. cit.

[2] O. Becker: Ueber den Wirbel und Kernbogen in der menschlichen Linse, Archiv f. Augenheilkunde, Bd. XII., 1883.

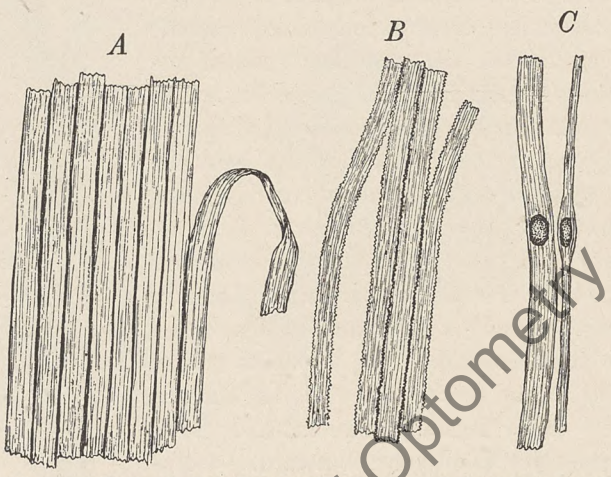
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capsule. In consequence of this, the nuclei of the young lens-fibres become progressively farther removed from the equator, their position within the so-called *nuclear zone* being indicated by the conspicuous *nuclear arch*, which is marked out by the sequence of the deeply staining nuclei.

The nuclear zone includes but a limited peripheral area near the margin of the lens, since the nuclei disappear from the more deeply situated fibres. The lens-whorl and nuclear arch depend upon the arrangement of the young developing lens-fibres derived from the elongating elements of the anterior epithelium, and are, therefore, most conspicuous during the years of active growth; in subjects of advanced years, on the contrary, they are but feebly marked.

The delicate subepithelial stratum of albuminous material which, in the fresh lens, lies between the posterior surface of the epithelium and the ante-

FIG. 91.



Fragments of isolated lens-fibres.—*A*, from the superficial layers; *B*, from a more centrally situated zone; *C*, parts of younger fibres, containing nuclei. Magnified 300 diameters.

rior ends of the lens-fibres, occupies the space which represents the remains of the cavity of the primary lens-sac. During life it is probable that this substance is semi-fluid; it rapidly liquefies after death, when its presence may be demonstrated, on puncture of the anterior capsule and epithelium, by the extrusion of a droplet of the so-called *liquor Morgagni*. The latter, according to O. Becker, never exists during life. Abnormal dilation of the capillary subepithelial space, owing to imbibition of fluid, and vacuolization of its albuminous contents are also frequent post-mortem changes.

The *substance of the lens* consists of an aggregation of the lens-fibres united by the intervening cement-substance. The lens-fibres represent the greatly elongated, specialized epithelial cells, primarily of the posterior wall of the lens-sac, supplemented by those derived from the anterior epithelium. The individual elements, as seen after isolation by means of boiling, prolonged maceration in acids, or other methods, are long, flattened, ribbon-like

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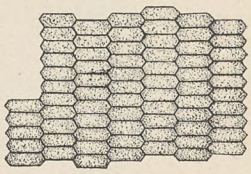
fibres which present in transverse section a compressed hexagonal outline. The longer parallel sides face outward and inward, while the shorter boundaries converge at either edge.

The length of the lens-fibres composing the superficial layers is much greater than that of those centrally situated, since the former extend about two-thirds of the meridional distance from pole to pole, while the latter correspond closely to the length of the lens-axis; the peripheral fibres measure, therefore, about eight millimetres, and the central ones four millimetres, or about half as much. Additional variations in the breadth and the thickness of the fibres are exhibited by the superficial and axial elements: the former measure from .010 to .012 millimetre in width and about .005 millimetre in thickness, the latter only about .0075 millimetre and .0025 millimetre for the corresponding dimensions.

Further differences between the central and the superficial lens-fibres are emphasized by the nucleus, which structure is present in the peripheral fibres, but absent in those axially placed. The position of the nucleus, when present, is indicated in profile views of the elements by a localized increase in the thickness of the fibre; the width of the fibre, on the other hand, is sufficient to accommodate the nucleus without modifying the contour. The superficial fibres are further distinguished from those occupying the centre of the lens by being softer and containing more fluid, the axial fibres exhibiting the results of a process of hardening somewhat analogous to that observed in the outer layers of the epidermis.

The peripheral lens-fibres present a smooth outline in contrast to the serrated edges of those forming the middle and inner portions of the lens. The finely toothed borders of the fibres are not uniformly developed on all edges, but are usually best marked on the diagonally opposed blunter edges. The serrations are so disposed that they do not interlock, but are only in apposition along the apices of the minute projections, the union of the lens-fibres being effected by the interfibrillar cement-substance. The minute intervals left between the individual lens-fibres in consequence of the arrangement of the abutting serrations are occupied by the semi-fluid cement-substance. While these tracts constitute passage-ways of importance for the transmission of nutritive juices to the tissue of the lens, they do not constitute a system of interfibrillar canals as described by v. Becker,[1] but correspond to the intercellular clefts found in other epithelial structures. Schlösser[2] not only regards these spaces as lymph-paths, which in principle they indeed

FIG. 92.



Lens-fibres seen in transverse section. Magnified 350 diameters.

[1] F. v. Becker: Untersuchung über den Bau der Linse bei den Menschen und den Wirbelthieren, Archiv f. Ophthalmol., Bd. IX., 1863.

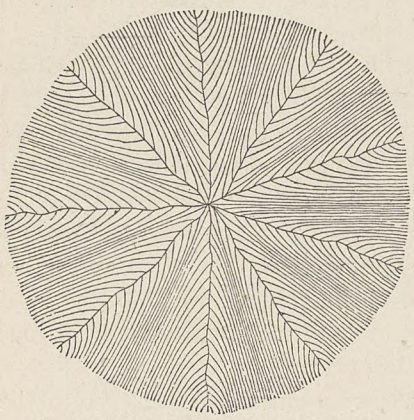
[2] Schlösser: Ueber die Lymphbahnen der Linse, Münchner med. Wochenschrift, Bd. XXXVI., 1889.

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are, but ascribes to their contents a definite current, quoting the clinical observations of Samelsohn on the dissemination of rust particles along the interfibrillar clefts in support of his views. The bond of union between the individual lens-elements differs in its stability on the several sides of the fibres, since the layer of cement-substance is thinnest between the broader surfaces of the fibres and thickest over the narrow facets.

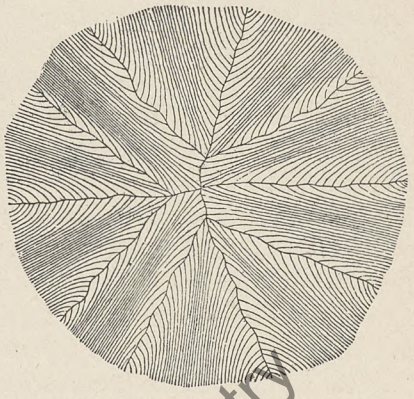
The *cement-substance* resembles that occurring in other epithelial structures, being semi-fluid in consistence and albuminous in nature; in addition to uniting the individual lens-fibres with one another, it exists in other localities, as beneath the anterior epithelium and between the ends of the

FIG. 93.



Central part of the anterior lens-star, showing close relations of lines of juncture in perfectly preserved tissue. (Babuchin.)

FIG. 94.



Central part of the posterior lens-star, showing union of lines of juncture of lens-fibres. (Babuchin.)

abutting fibres along the so-called sutures. The presence of considerable quantities of interfibrillar substance in the form of a stellar mass, and along its diverging limbs, constituting the lens-stars, later to be noted, as described by the older anatomists and represented in the classic drawings of Arnold,[1] depends upon post-mortem changes, no such accumulations of interfibrillar substance existing within the living lens or within the perfectly preserved tissue. The investigations of Zernoff,[2] Babuchin,[3] O. Becker,[4] and others show conclusively the fallacy of the older descriptions.

In addition to the variation in the consistence of the peripheral and of the centrally situated fibres, already noted, each lens-element exhibits individual differences in the softness and greater affinity for stains possessed by

[1] F. Arnold: Tabulæ anatomicæ, Fasciculus II.; Icones organorum sensum, Tab. III., 1838.

[2] Zernoff: Zum mikroskopischen Bau der Linse beim Menschen und bei den Wirbelthieren, Archiv f. Ophthalmol., Bd. XIII., 1867.

[3] Babuchin: Die Linse, Stricker's Handbuch der Lehre von den Geweben, Bd. II., 1872.

[4] O. Becker: Ueber den Wirbel und Kernbogen in der menschlichen Linse, Archiv f. Augenheilkunde, Bd. XII., 1883.

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the extremities of the fibres, as compared with the middle portions; likewise by the axial portion of the fibre as contrasted with the denser superficial zone. A distinct demarcation between these parts of the fibre, however, does not exist, these changes in the physical character of the lens-elements occurring gradually and not abruptly. While the peripheral or superficial substance of each fibre is somewhat condensed and thereby constitutes a boundary zone, no distinct membrane envelops the lens-fibre. Interesting changes in the contour of the lens-fibres due to variations in their consistence are figured in the paper of Ritter.[1]

Fig. 95.

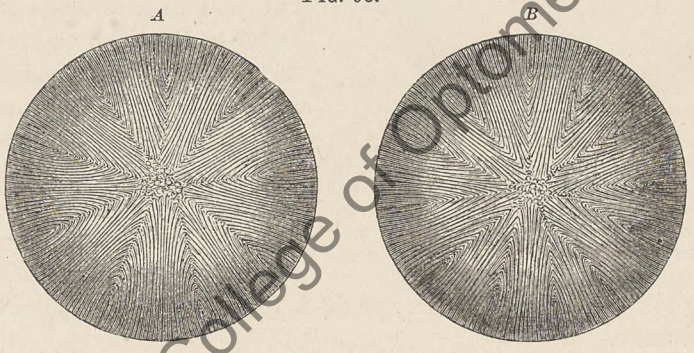


Crystalline lens of new-born child, seen from the side, showing the course of the lens-fibres. (Arnold.) Magnified 6 diameters.

After hardening and removal of the capsule, the lens may be readily separated into a number of concentric lamellæ in a manner somewhat similar to the separation taking place in the cleavage of the coats of an onion. The laminæ thus obtained, however, are not continuous sheets including the entire lens, but break up into segments which at most include only about one-third, not infrequently distinctly less, of the lens-surface.

The fracture of the lamellæ in a definite manner depends upon the arrangement of the lens-fibres, and corresponds to the lines along which these elements abut, as presently to be described. The lines of apposition

Fig. 96.



Adult crystalline lens, showing lens-stars. (Arnold.)—*A*, anterior surface; *B*, posterior surface. The radiating lines of juncture meet at the central area apparently occupied by an indifferent granular substance. Magnified 6 diameters.

of the fibres, or suture-lines, appear as faintly marked, whitish, radiating striæ, which depend upon the local accumulations of the interfibrillar cement-substance and constitute the lens-stars.

The *lens-stars* are best seen in the fœtal lens or in the centre of the

[1] Ritter: Zur Histologie der Linse, Archiv f. Ophthalmol., Bd. xxii. u. xxiii., 1876, 1877.

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adult lens, where they appear on both surfaces as triradiate figures the arms of which extend from the centre towards the periphery. They are symmetrically disposed, and diverge from one another at a uniform angle of 120°. The rays of the two surfaces do not correspond in position, but are so arranged—as well seen in the lens of the new-born child and less distinctly in the nucleus of the adult lens—that on the anterior surface the upper ray is vertical, while on the posterior surface the lower ray stands perpendicularly. It follows from this relation that the rays of the anterior star have undergone a torsion of 60° in reaching the posterior surface, or, in other words, that the position of the points of contact of the lens-fibres changes in each successive stratum, so that their lines of apposition become spiral.

In the adult lens the star figures become less symmetrical and more complicated by the introduction of secondary rays; these are so placed that the lens-stars possess five, six, or more arms. The exact arrangement, both as to number and disposition of the radii, is variable, although the basis of the figures, as shown by the lens-stars of the nuclear portion of the lens, still represents the now masked primary plan. Friedenberg[1] found the five-rayed star most common in the adult lens. The rays, in the fully matured condition, do not extend as far as the centre of the poles, but join in a common area, the *stellar mass*, which appears granular, as usually seen, and is somewhat irregular in outline. The appearance of the secondary radii is due to the juncture-line of the additional lens-fibres necessitated by the increased circumference of the growing lens, the number sufficing to cover in the periphery of the fœtal lens no longer possessing the requisite space.

FIG. 97.

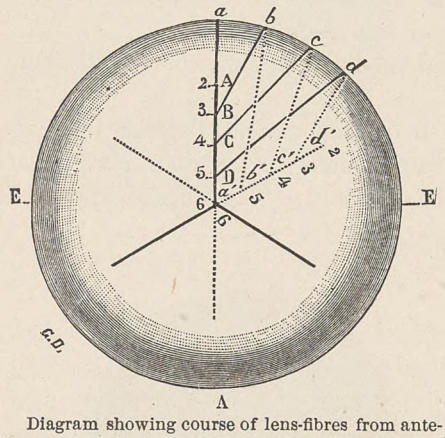


Diagram showing course of lens-fibres from anterior to posterior stars. (Testut.)—*E*, *E*, equatorial axis; the dark lines represent the anterior star, the dotted lines the posterior; the course of the individual fibres *A*–*D* is indicated to *a'*–*d'*.

The complicated disposition and course of the lens-fibres have already been mentioned in connection with the description of the lens-stars: it remains here to consider the arrangement of the fibres more in detail.

With the exception of those forming the immediate core of the lens, the direction of which corresponds closely with the lens-axis, the general course of the fibres is meridional, the ribbon-like elements extending

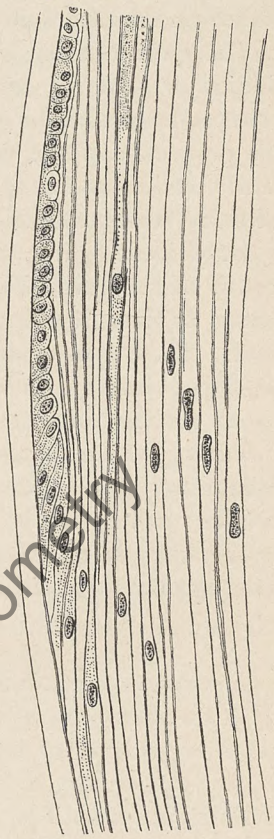
1 Friedenberg: Ueber die Sternfigur der Krystalllinse, Inaug. Dissertation, Strassburg, 1891.

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from the anterior to the posterior surface. The anterior end of the fibre lies within some part of the star of the corresponding surface, extends to the periphery of the lens, around which it sharply bends, and passes to some point within the system of the stellar figure of the posterior surface. Those fibres which begin near the anterior pole proceed to the more peripheral parts of the posterior star, and, conversely, those lying near the margin anteriorly reach farther towards the posterior pole.

The lens being formed by the superposition of consecutive strata of fibres, it follows that the curvature as well as the length of the elements composing the various layers must differ, those constituting the more superficial portions of the lens being more sharply bent and longer than those occupying a position nearer the nucleus. The elements of the same stratum, however, possess the same length and curve. The curvature and length of the fibres gradually decrease towards the centre; the elements occupying the middle layers, or about the outer limit of the nucleus, present almost the curvature of a sphere, those lying axially possessing progressively diminishing flexure and length until the central fibres, as already stated, are almost straight and of equal length with the antero-posterior diameter of the lens.

FIG. 98.



Meridional section of equatorial region of crystalline lens of a woman aged seventy-five years. (Becker.) The inactivity of the transformation zone is conspicuous in contrast with that of the young lens.

The course of the lens-fibres is not strictly meridional throughout, since the fibres join the suture-lines at angles approaching ninety degrees; the fibres, therefore, usually undergo additional bending just before they join the rays, in consequence of which their course *in situ* often approaches an S-like curve. As the result of this bending towards the lines of cement-substance, the fibres turn in such manner that collectively they form peculiar figures between the radii, to which the term *vortex lentis* has been applied.

It follows from the arrangement of the elements above described that the subcapsular epithelium comes in contact with the broader surface of the lens-fibres, and nowhere, except throughout a limited equatorial area, with the ends of the fibres, since these abut within the star-rays against one another. Meridional sections of the lens, therefore, invariably show the superficial lens-fibres running parallel with the anterior epithelium, to which they are united by the intervening cement-substance. At one point, however, where

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the epithelial cells undergo transition into the elongated lens-fibres at the equatorial margin, the ends of the young fibres come in contact with the anterior epithelium within a limited area; this disposition is soon replaced by the usual relation, in consequence of the rapid growth of the lens-fibres and their increasing convexity.

In preparations of silvered lens and capsule, in addition to the somewhat complicated mosaic produced by the cells on the anterior capsule, the posterior capsule, as noted by Barabaschew,[1] also exhibits the impressions of the lens-fibres, as well as aberrant markings due to the silver reduction effected by extruded fluid substances.

The growth of the lens after its primary formation takes place by the addition of strata of new fibres, principally in the equatorial region, in correspondence with the great cellular activity within the transition zone. The production of the new elements necessary to maintain the continual transformation of the epithelial cells into lens-fibres is found within the anterior epithelium alone, the elements of which, as shown by the presence of karyokinetic figures, undergo division and produce new cells during the growth of the lens. The new cells are gradually displaced towards the equator by the still younger elements, and in turn become transformed into fibres. There is no evidence of division and multiplication directly of the lens-fibres, these elements being in a condition of high specialization and beyond the stage of reproductive activity. According to the investigations of Harting,[2] the embryonal lens increases by interstitial growth, the individual fibres gaining in size; after birth, however, as shown originally by Kölliker[3] and by Henle,[4] the further growth of the lens is by apposition, the new fibres being added by the transformation of the anterior epithelium at the equatorial transition zone.

THE VITREOUS BODY.

The large space included between the lens in front and the retina behind and at the sides, embracing approximately four-fifths of the capacity of the eyeball, is occupied by the vitreous body.

The *vitreous body*, or *humor vitreus*, when examined in the perfectly fresh condition, is a beautifully transparent, semi-fluid mass, the general form of which resembles a sphere flattened in its antero-posterior axis; the anterior pole is further modified by a depression, the *fossa patellaris*, which receives the posterior surface of the lens. An important function of the vitreous body is the support of the retina, against which it closely lies, but from which it is readily separable after appropriate treatment; at one point,

[1] Barabaschew: Beitrag zur Anatomie der Linse, Archiv f. Ophthalmol., Bd. XXXVIII., 1892.

[2] Harting: Recherches micrométriques, 1847.

[3] Kölliker: Ueber die Entwickelung der Linse, Zeitschrift f. wiss. Zoologie, Bd. VI., 1855.

[4] Henle: Zur Entwickelungsgeschichte der Krystalllinse und zur Theilung des Zellkerns, Archiv f. mik. Anatomie, Bd. XX., 1882.

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however,—namely, over the optic entrance,—the vitreous and the retina are more intimately connected than elsewhere, in consequence of the close association established by the early entrance of the hyaloid in this location.

This remarkable and conspicuous constituent of the eyeball early attracted the attention of anatomists, and from the observations of Petit, Demours, Zinn, Cloquet, Fr. Arnold, Brücke, Hannover, and Bowman to the investigations of Schwalbe, Iwanoff, H. Virchow, Straub, and Retzius, a period of almost one and three-quarters centuries, the structure of the vitreous body has been the subject of widely divergent opinions, and even at the present, it must be admitted, conflicting views remain to be reconciled.

The descriptions of the vitreous by the earlier anatomists, handicapped as they were by the inadequacy of the methods at their disposal, pertained chiefly to the macroscopic appearances: the papers of Bowman,[1] in 1848, and of Virchow,[2] in 1852, may be said to mark the beginning of the studies really devoted to the minute structure of the vitreous.

Examination of the fresh tissue was soon supplemented by inspection of frozen eyes, and later by study of the vitreous after treatment with solutions of various chromic acid salts. Among the most important results of the early investigations was the establishment by F. Arnold[3] of the existence of a distinct limiting membrane, the *hyaloidea*, bounding the exterior of the vitreous, the presence of which had been surmised by Demours[4] and Zinn.[5] Arnold also accepted the teachings of these authors, that the external membrane sent numerous prolongations inward which served to divide the vitreous into thin-walled compartments or "cells" containing the watery constituents.

Pappenheim[6] and Brücke,[7] from consideration of the effects of certain chemical solutions (potassium bichromate and lead acetate), advanced the view that the vitreous body consisted of a number of concentrically disposed lamellæ. Hannover,[8] about the same time, while accepting a somewhat similar concentric lamellation for the vitreous of mammals, described that of man as composed of radially arranged sectors. Two rival views—the concentric or "onion" and the radial or "orange" theory—were thus offered the student at the close of the first half of the present century, each being warmly supported by its own adherents. Bowman,[9] Virchow,[10] and

[1] Bowman: Observations on the Structure of the Vitreous Humor, Dublin Quart. Journal of Med. Science, 1848.

[2] Virchow: Ueber den menschlichen Glaskörpers, Virchow's Archiv, Bd. IV. u. V., 1852–53.

[3] F. Arnold: Anatomische und physiologische Untersuchungen über das Auge des Menschen, 1832.

[4] Demours: Observation anatomique sur la structure cellulaire du corps vitré, Mém. de Paris, 1741.

[5] Zinn: Descriptio anatomica oculi humani, 1755.

[6] Pappenheim: Die specielle Gewebelehre des Auges, 1842.

[7] Brücke: Ueber den inneren Bau des Glaskörpers, Müller's Archiv, 1843.

[8] Hannover: Entdeckung des Baues des Glaskörpers, Müller's Archiv, 1845.

[9] Bowman: loc. cit.

[10] Virchow: loc. cit.

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Kölliker,[1] a few years later, questioned the correctness of both these theories, and advanced the opinion, based upon microscopical examination of fœtal as well as adult tissue, that the vitreous contained structural elements represented by fibres and cells; Virchow further maintained that the vitreous in general corresponded to a gelatinous or mucoid connective tissue, resembling the jelly of Wharton of the umbilical cord in the possession of irregular cells and a homogeneous intercellular substance.

The fact that the vitreous body consists of two parts—the fluid and the firmer constituents—is readily demonstrated by filtration, the substances remaining upon the filter representing the morphological elements. The latter, however, comprise but an insignificant part of the entire mass, since, as shown by Lohmeyer,[2] of one hundred parts by weight of vitreous substance, only from .021 to .07 part remain on the filter. The readiness with which the fluid portion of the vitreous drains away also shows the fallacy of the older views that the vitreous fluid was contained within membranous compartments.

In chemical composition the vitreous substance consists almost entirely of water, which, according to Berzelius,[3] Frerichs,[4] and Lohmeyer, constitutes from 98.40 to 98.64 per cent. of the whole. The remaining small proportion, composed of solids, includes salts, extractives, and traces of proteids and nucleo-albumin.

The soft, semi-fluid, gelatinous substance of the vitreous is enclosed within a distinct envelope, the hyaloid membrane, throughout a large part of its extent, which defines the relations of the collapsible vitreous mass to the surrounding parts; the vitreous body, therefore, may be regarded as consisting of two portions, the *substance proper* and its *capsule*.

The Vitreous Substance.—The investigations of Virchow and of Kölliker, to which reference has been already made, called attention to the presence of fibres and cells within the apparently homogeneous vitreous substance. The reticulated character of the vitreous framework described by the first of these authorities was accepted by Weber,[5] but Ciaccio[6] and H. Virchow[7] first strongly emphasized the richness of the fibrillation existing throughout this structure, although both Henle[8] and Blix[9] had

[1] Kölliker: Mikroscopische Anatomie, Bd. II., 1854.

[2] Lohmeyer: Beiträge zur Histologie und Aetiologie der erworbenen Linsenstaare, Zeitsch. f. ration. Medicin, N. F., Bd. V., 1854.

[3] Berzelius: Lehrbuch der Chemie, Bd. IX., 1831.

[4] Frerichs: Ueber Linsenstaare, Hannover'sche Annalen, 1848.

[5] C. O. Weber: Ueber den Bau des Glaskörpers und die pathologischen, namentlich entzündlichen Veränderungen desselben, Virchow's Archiv, Bd. XIX., 1860.

[6] Ciaccio: Beobachtungen über den inneren Bau des Glaskörpers im Auge des Menschen und der Wirbelthiere im Allgemein, Moleschott's Untersuchungen zur Naturlehre, Bd. X., 1870.

[7] H. Virchow: Die morphologische Natur des Glaskörpergewebes, Bericht über d. 17. Versamml. d. Ophthalmologischen Gesellschaft, Heidelberg, 1885.

[8] Henle: Eingeweidelehre, Handbuch d. Anatom. d. Menschen, Bd. II., 1866.

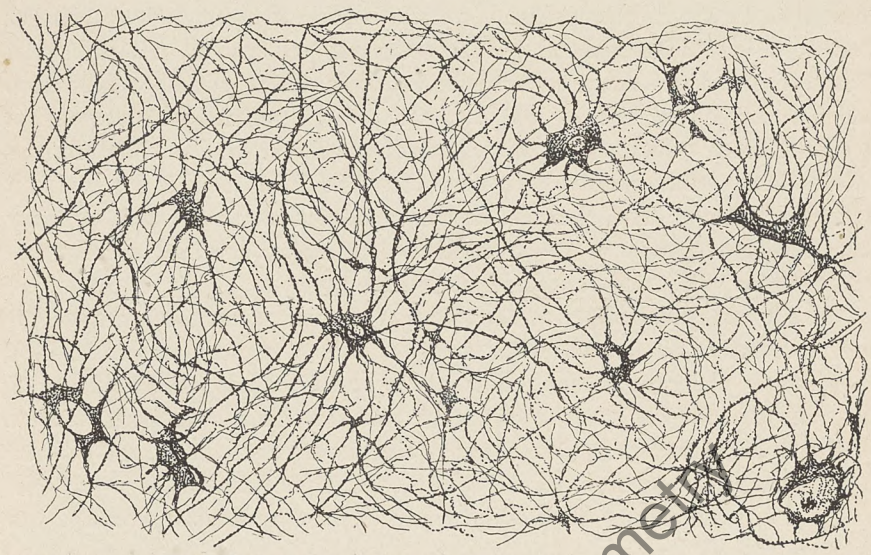
[9] Blix: Studier öfver glaskroppen, Medicinskt Archiv, Bd. IV., 1868.

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recorded the observation of net-works of delicate fibres. Other observers accepting more or less provisionally the existence of a supporting framework of fibres are Merkel,[1] Schiefferdecker,[2] Rauber,[3] and Schäfer.[4]

Divergent views, however, have not been wanting, among which those of Stilling,[5] Iwanoff,[6] Schwalbe,[7] and Toldt[8] in common recognize a differentiation of the vitreous body into a peripheral or cortical portion, concentrically lamellated, and a central or nuclear portion which possesses a

FIG. 99.



Portion of vitreous substance of six months' human fœtus, showing stellate cellular elements which contribute to form the framework. (Retzius.) Magnified 450 diameters.

radial arrangement. These authors, however, differ from the older anatomists in their interpretation of the significance of the peripheral lamellation, since they regard the cleavage as dependent upon minute interlamellar clefts, without distinct walls, rather than upon the presence of membranous partitions. In his subsequent descriptions,[9] Schwalbe aptly compares the vitreous substance to a sponge saturated with fluid, and declares that histologically the adult vitreous substance is to be regarded neither as a form

[1] Merkel: Handbuch der topographischen Anatomie, Bd. I., 1887.

[2] Schiefferdecker und Kossel: Gewebelehre, Bd. II., 1891.

[3] Rauber: Lehrbuch der Anatomie des Menschen, 4te Aufl., Bd. II., 1894.

[4] Schäfer: The Sense Organs, Quain's Anatomy, 10th ed., vol. III., Pt. 3, 1894.

[5] Stilling: Eine Studie über den Bau des Glaskörpers, Archiv f. Ophthalmol., Bd. XV., 1869.

[6] Iwanoff: Der Glaskörper, Stricker's Handbuch der Lehre von den Geweben, Bd. II., 1872.

[7] Schwalbe; Der Glaskörper, Graefe u. Saemisch's Handbuch der gesammten Augenheilkunde, Bd. I., 1874.

[8] Toldt: Lehrbuch der Gewebelehre, 3te Aufl., 1888.

[9] Schwalbe: Lehrbuch der Anatomie der Sinnesorgane, 1887, S. 140.

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of mucoid tissue nor as a transudate, "but as a connective tissue exceptionally rich in water, the fixed cells of which have been lost, and whose interfibrillar substance, largely infiltrated with water, is invaded by migratory cells."

Study of the fœtal condition of the vitreous body is of much importance as affording trustworthy information as to the primary arrangement and the morphological significance of its structure in the adult. Examination of rabbit embryos of from thirteen to fifteen days shows the primary vitreous to be represented by an irregular reticulum of branched mesodermic cells lodged within a relatively large amount of homogeneous matrix or ground-substance. These elements are undoubted embryonal forms of connective-tissue cells the ancestors of which gained entrance into the interior of the eye by the ingrowth of the perivesicular mesoderm. While Keibel[1] denies that the ingrowth of any mesoderm beyond the blood-vessels takes place, other observers, including Kölliker,[2] Bonnet,[3] Hertwig,[4] Minot,[5] and Schenk,[6] agree in recognizing that such primary intra-ocular inclusion of the mesoderm does occur, in which opinion the observations of the writer lead him to share.

The primary condition of the vitreous, therefore, represents an embryonal connective tissue; the later stages of this structure are marked by conspicuous changes, among which the almost complete disappearance of the cells and the infiltration of the ground-substance by a large amount of fluid are prominent. Coincidently with the suppression of the cellular elements the formation of delicate fibrillæ takes place, so that it is possible, although by no means easy, even within the fresh vitreous substance, to distinguish cells and fibres as the morphological constituents of the beautifully transparent tissue.

After treatment with suitable preservatives, however, as Müller's fluid, solutions of chromic acid, Flemming's solution, or sublimate solution, and subsequent staining, the demonstration of these elements becomes far more certain and satisfactory. In preparations of such character the fibrillæ, which are particularly conspicuous, are seen to constitute in general a supporting felt-work in the interspaces of which are lodged the more fluid parts of the vitreous substance.

The *fibrillar framework* of the adult human vitreous consists of an interlacement of delicate threads which vary somewhat in thickness and in contour according to the method of preservation of the tissue. While

[1] Keibel: Zur Entwickelung des Glaskörpers, Archiv f. Anat. u. Physiolog., 1886.

[2] Kölliker: Grundriss der Entwickelungsgeschichte der Menschen und der höheren Tiere, 2te Aufl., 1884.

[3] Bonnet: Grundriss der Entwickelungsgeschichte der Haussäugethiere, 1891.

[4] Hertwig: Lehrbuch der Entwickelungsgeschichte des Menschen und der Wirbelthiere, 3te Aufl., 1890.

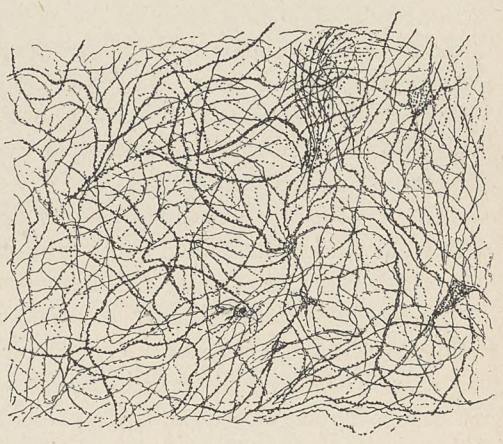
[5] Minot: Human Embryology, 1892.

[6] Schenk: Lehrbuch der Embryologie des Menschen und der Wirbelthiere, 2te Aufl., 1896.

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fibrillæ may undoubtedly be demonstrated in the fresh vitreous, their display in tissue hardened in solutions containing chromic acid or its salts is much more certain and complete.

Fig. 100.



Portion of vitreous substance from adult, showing the dense felt-work of fibres and the absence of cells: only atrophic traces of the latter are seen. (Retzius.) Magnified 450 diameters.

The extent, however, to which these preserving fluids may affect the albuminous, almost fluid, matrix must be taken into account in estimating the richness of the fibrillar network during life, since it is possible, and the writer believes probable, that the action of the reagent is responsible for the production of at least a part of the densely felted, delicate fibrillæ seen in certain preparations. The experiments of the writer[1] on the effect of treating albuminous fluids with solutions of potassium bichromate, chromic acid, etc., emphasize the production with certainty of fibrillar structures of great perfection and complexity under such conditions.

The vitreous fibrillæ, as described by Retzius,[2] who regards the appearances seen in preparations treated with Flemming's solution as entirely trustworthy as representing the normal structure, occur throughout all parts of the vitreous substance, and form by their interlacement, but not true anastomosis, a felting in which the interspaces are often so narrow as scarcely to equal the diameter of a red blood-cell. "Under high amplification the entire tissue is resolved into a felt-work of exceptional intricacy composed of the finest fibres, which cross one another in various directions and here and there join in narrow nodal points, without, however, constituting net-works."

According to Retzius, many fibres are beset with peculiar minute glistening spherules or granules of varying size; regarding the nature of these bodies the distinguished observer remains in doubt, although he rejects as untenable the supposition that their presence is attributable to the action of the reagents employed, since the intervening ground-substance remains homogeneous. The experiences of the writer, already noted, lead him, however, to regard these bodies as due to the effect of the reagents employed, since almost identical appearances may be artificially produced.

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[1] Piersol: Review of Heitzmann's Microscopical Morphology, Amer. Journal of the Med. Sciences, January, 1883.

[2] Retzius: Uber den Bau des Glaskörpers und der Zonula Zinnii in dem Auge des Menschen und einiger Thiere, Biolog. Untersuch., N. F., Bd. VI., 1894.

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With the advance of age from childhood to adult life the intricacy of the fibrillar framework may also undergo modification, since, as shown by Retzius, partial absorption usually takes place, especially in certain localities, thereby producing a framework of less density.

The central part of the vitreous body is modified by the presence of a distinct channel, the *canalis hyaloideus*, which extends from the optic papilla forward almost to the posterior surface of the lens-capsule, and represents the remains of the passage-way occupied by the fœtal hyaloid vessels in their transit from the optic entrance to the vascular capsule of the lens which they supply.

The *hyaloid canal*, *canal of Stilling*, *canal of Cloquet*, or *central canal*, as seen in the adult human eye, is a slightly compressed tubular channel, from one to two millimetres in diameter, which begins at the optic papilla with a slight enlargement, the *area Martegiani*, of equal width with the disk, and continues towards the posterior pole of the lens, in the vicinity of which it terminates in a blind, often somewhat dilated, extremity. In the fœtus the anterior termination of the canal is distinctly funnel-shaped, since the loose vascular connective tissue which it contains becomes continuous with the vascular lens-capsule. After the disappearance of the hyaloid artery, the canal contains the remains of the vascular structures and the surrounding delicate connective-tissue trabeculæ, which in later years are represented alone by the shrunken mass attached to the retina within the physiological excavation of the optic disk.

The limits of the hyaloid canal are defined by delicate membranous structures, which, however, are to be regarded, according to Retzius,[1] rather as the result of condensation of the fibrillar tissue of the vitreous substance than as a part of the hyaloid membrane, as frequently assumed. Haensell[2] recognizes three zones within that portion of the vitreous body of the newly-born child situated outside of the hyaloid canal,—(*a*) an inner condensed stratum contributing the wall of the central channel, (*b*) the vitreous substance proper, (*c*) an external condensed stratum, the future hyaloid membrane.

While the existence of membranous lamellæ throughout the vitreous substance cannot be accepted in the sense of the descriptions of the older anatomists, local thickenings and condensations of the fibrillar framework occur at various levels within the vitreous, as especially emphasized in the recent investigations of Retzius. Such thickenings of the usual vitreous tissue are particularly distinct, and often numerous, without, however, being regularly disposed in the anterior and lateral parts of the ball.

The *cellular elements* of the vitreous substance are of two kinds, the true connective-tissue cells and the migratory leucocytes: from the foregoing account of the origin of the vitreous it is evident that the con-

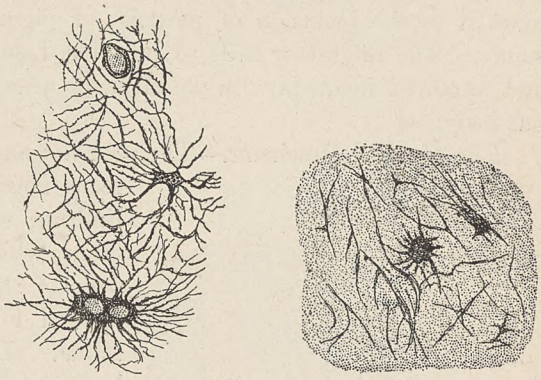
[1] Retzius: loc. cit., S. 82.

[2] Haensell: Recherches de la structure et l'histogénèse du corps vitré normal et pathologique, Paris, 1888.

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nective-tissue elements are far more numerous and conspicuous during the early stages of the tissue than later. In the vitreous of the new-born, Haensell[1] describes a protoplasmic net-work composed of the united processes of the young connective-tissue cells, while Retzius[2] figures richly branched stellate elements in the fœtal tissue.

Fig. 101.



Portions of adult vitreous substance, showing remains of vitreous cells in various stages of atrophy and fibrous metamorphosis. (Retzius.) Magnified 450 diameters.

Examination of the adult vitreous, on the contrary, shows the connective-tissue cells to be meagre and sparsely distributed and so inconspicuous that their presence is readily entirely overlooked. The sole representatives of the fair-sized connective-tissue cells of the early stages are minute, irregularly stellate or branched elements the protoplasm of which often exhibits cleavage into fine fibrillæ which take part in the constitution of the general fibrous framework. These vitreous cells are irregular in their distribution, and give the impression of being in various stages of a retrogressive process.

The *migratory leucocytes*, or *wandering cells*, occur within the adult vitreous in variable number, especially, however, immediately beneath the hyaloid membrane, where they constitute the so-called *subhyaloid cells*. That these elements are leucocytes which have invaded the vitreous substance is shown by their morphological identity, including amœboid movement, with the colorless cells of the circulation, and by the fact that they occur in particular profusion in those localities, as in the vicinity of the ora serrata and the optic entrance, where the proximity of blood-vessels favors the entrance of leucocytes into the vitreous tissue.

Iwanoff[3] divided the wandering cells within the vitreous into three groups: 1, round cells resembling the peripheral subhyaloid elements; 2, stellate or spindle-cells, with a single or several nuclei and extended processes; 3, vacuolated cells, which, in addition to one or more nuclei, contained a vacuole, sometimes two, filled with fluid. While Iwanoff regarded these elements as distinct varieties, other observers, including Pagenstecher and Schwalbe, recognized that all the migratory cells were but different

[1] Haensell: Recherches sur le corps vitré, Bulletin de la clinique nationale ophthalmique de l'hospice des Quinze-Vingts, t. iv., 1886.

[2] Retzius: loc. cit., Tafel xxix., Fig. 3.

[3] Iwanoff: Zur normalen und pathologischen Anatomie des Glaskörpers, Archiv f. Ophthalmol., Bd. xi., 1865.

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forms and conditions of the same elements, the leucocytes. Schwalbe[1] experimentally demonstrated the correctness of his interpretation by introducing portions of mammalian vitreous into the lymph-sacs of frogs, and subsequently noting the entrance of the amphibian leucocytes, previously marked by the inclusion of particles of pigment, into the vitreous substance. The migratory cells so introduced assumed all the various forms and appeared identical with the elements usually encountered in the vitreous body.

The Hyaloid Membrane.—The posterior and lateral portions of the vitreous mass are invested by a distinct limiting structure, the hyaloid membrane, which appears as an extremely delicate structureless envelope closely applied to the inner surface of the retina. In the earliest years this limiting membrane is wanting, and, indeed, its presence even in the adult eye has been questioned by some anatomists, among whom is Merkel,[2] who regards the structure as artificially produced.

FIG. 102.



Surface view of fragment of hyaloid membrane from adult eye, showing a number of adherent subhyaloid cells. (Retzius.) Magnified 330 diameters.

The presence of the hyaloid can be readily demonstrated in eyes which have lain for a couple of days after death, or been preserved for several days in dilute alcohol. In such preparations the vitreous body may be readily detached from the surrounding nervous tunic without mutilation, and on careful inspection the existence of a delicate investment be shown by the definite boundary of the separated mass and the minute folds on its free surface. The separation thus effected also emphasizes the fact that the hyaloid membrane belongs to the vitreous body and not to the retina, as maintained by Iwanoff[3] and others, although, as shown by O. Schultze,[4] the hyaloid is primarily genetically related to the retinal tunic.

The immediate formation of the hyaloid is effected by the metamor-

[1] Schwalbe: Der Glaskörper, Graefe und Saemisch's Handbuch d. gesammten Augenheilkunde, 1874, Bd. I. S. 474.

[2] Merkel: Handbuch der topographischen Anatomie, 1887, Bd. I. S. 266.

[3] Iwanoff: Der Glaskörper, Stricker's Handbuch der Lehre von den Geweben, Bd. II., 1871.

[4] O. Schultze: Zur Entwickelungsgeschichte des Gefäss-Systems im Säugethierauge, Kölliker's Festschrift, 1892.

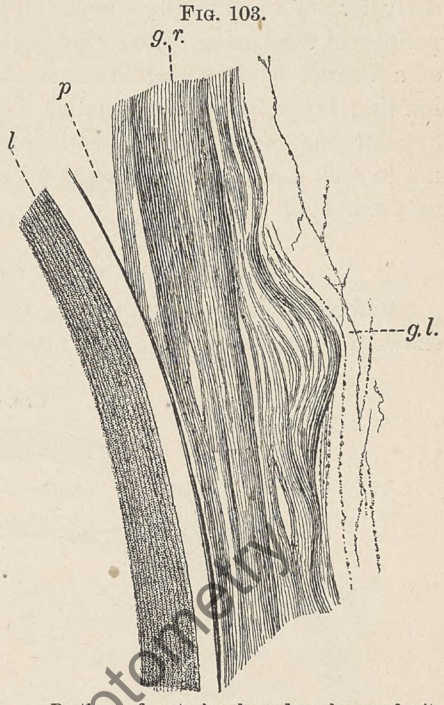
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phosis of the layer of mesodermic tissue covering the periphery of the vitreous substance. According to Haensell,[1] a transient endothelial structure precedes the completed hyaloid envelope.

Concerning the relations between the hyaloid membrane and the anterior surface of the vitreous body opinions by no means accord, since this question depends so closely for its solution on the broader and greatly mooted one regarding the details of the participation of the hyaloid membrane in the formation of the suspensory apparatus of the lens.

Anticipating briefly for our present purpose some of the facts to be discussed more at length in connection with the zonula, two opposed views as to the behavior of the hyaloid in the vicinity of the ora serrata must be noted. Ignoring the individual views of the older anatomists, it may be recalled that it was generally accepted that beyond the ora serrata the hyaloid splits into an outer and an inner layer which respectively are attached to the anterior and the posterior lens-capsule, the entire hyaloid membrane being devoted to the formation of the suspensory apparatus of the lens.

FIG. 103.



Portion of anterior boundary layer of vitreous body of adult. (Retzius.)—*g.r.*, distinctly laminated boundary zone; *g.l.*, adjoining vitreous substance; *l*, portion of posterior lens-surface, *p*, lies within the so-called Petit's canal. Magnified 330 diameters.

In opposition to the preceding and generally accepted opinion, Henle[2] maintained that the zonula was the continuation of the outer layer into which the hyaloidea separates at the border of the ciliary body, the inner lamella following the anterior surface of the vitreous body and investing the patellar fossa. Among the more recent writers, Stuart[3] and Schäfer[4] also accept the existence of a lamella of the hyaloid membrane over the anterior surface of the vitreous, while opposed to this view the opinion of Retzius[5] is especially emphatic.

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[1] Haensell: Recherches de la structure et l'histogénèse du corps vitré normal et pathologique, Paris, 1888.

[2] Henle: Eingeweidelehre, Anatomie des Menschen, 2te Aufl., Bd. II., 1873, S. 697.

[3] Stuart: On a Membrane lining the Fossa Patellaris of the Corpus Vitreum, Proceedings of the Royal Society, vol. XLIX., 1891.

[4] Schäfer: The Eye, Quain's Anatomy, 10th ed., vol. III., Pt. 3, 1894.

[5] Retzius: loc. cit., S. 83.

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That the anterior portion of the periphery of the vitreous substance, uncovered by the hyaloid membrane, possesses a definite boundary is not to be questioned, since the presence of such a lamella is readily demonstrated in suitably prepared sections: critical study of this limiting structure, however, shows it to be formed, as maintained by Retzius, and, indeed, long before by Iwanoff, by a condensation of the vitreous substance, and not as a derivative of the laterally situated hyaloid. Merkel[1] likewise recognizes a peripheral thickening of the vitreous tissue, although he rejects the presence of a distinct hyaloid membrane at any point. According to Retzius, the limiting layer lining the patellar fossa consists of a condensation of the fibrillar framework of the vitreous substance: a similar thickening, although not to such a conspicuous degree, takes place in the production of the wall of the hyaloid canal.

THE SUSPENSORY APPARATUS OF THE LENS.

Reference to the accompanying diagrammatic section of the human eye shows that the periphery of the lens is connected with the adjacent annular

FIG. 104.

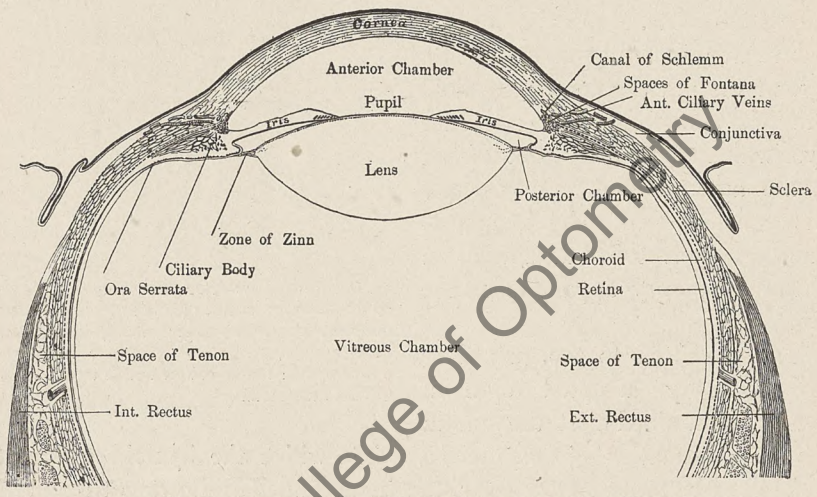


Diagram of anterior segment of eye, drawn to accurate scale. (Flemming.)

series of ciliary processes by means of delicate bands which pass from the vicinity of the ora serrata over the ciliary body to the margin of the lens. These trabeculæ collectively constitute the suspensory ligament or zone of Zinn, a structure of much importance in maintaining the position of the lens and in effecting changes in its curvature.

The *zone of Zinn*, or *zonula ciliaris*, appears as a delicate annular structure, about six millimetres in width, encircling the border of the lens and stretching from the latter point to the ora serrata. As seen in meridi-

[1] Merkel: Handbuch der topographischen Anatomie, Bd. I., 1887, S. 266.

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onal sections of the human eye, the zonula is composed of an interlacement of conspicuous fibres which span at various angles the interval between the lens and the ciliary processes.

The origin of these fibres and the relations of the zonula to the adjacent parts of the eye have long engaged the attention of anatomists, but, notwithstanding the numerous investigations undertaken by competent observers, opinions are far from settled as to many details in the constitution of these parts. As already incidentally noted, the question concerning the anterior relations of the hyaloid membrane is inseparably connected with that of the origin of the zonular fibres.

The older view, according to which the hyaloid membrane beyond the ora serrata splits into two lamellæ which are continued as the zonula to the anterior and posterior surfaces of the lens-capsule, was for a long time very generally accepted, and even yet Schwalbe[1] regards the zone of Zinn as the direct membranous prolongation of the thickened hyaloid.

It is especially due to the observations of Merkel,[2] Gerlach,[3] Czermak,[4] Topolanski,[5] and Garnier[6] that our conceptions regarding the constitution of the zonula have been modified, since they emphasized the fact that the zone of Zinn, formerly regarded as a membrane, is entirely composed of fibres which are independent structures and not parts of the hyaloid membrane. The latter, while closely associated with the zonula and giving origin to many of the zonular fibres, is continued over the orbiculus ciliaris on to the ciliary body as the extremely delicate homogeneous cuticular or glassy membrane covering these parts.

In estimating the closeness of the relations between the vitreous substance and the zonular fibres, it is of importance to recall the intimate genetic association between the two. It may be assumed as established that the primitive zonular fibres are earliest formed in the anterior portion of the developing vitreous substance, from which they proceed towards the immature ciliary body. As pointed out by Retzius,[7] the tissue occupying the funnel-shaped area surrounding the hyaloid canal is especially concerned in the production of the zonular fibres. These are at first very numerous and of extreme delicacy, later, as shown by Czermak,[8] becoming reduced in number and increased in size. With the limitation of the vitreous substance proper, the loose connective tissue associated with the hyaloid artery

[1] Schwalbe: Lehrbuch der Anatomie der Sinnesorgane, 1887.

[2] Merkel: Die Zonula ciliaris, Habilitationsschrift, 1870.

[3] Gerlach: Beiträge zur normalen Anatomie des menschlichen Auges, 1880.

[4] Czermak: Zur Zonulafrage, Archiv f. Ophthalmol., Bd. XXXI., 1885.

[5] Topolanski: Ueber den Bau der Zonula und Umgebung nebst Bemerkungen über das albinotische Auge, Archiv f. Ophthalmol., Bd. XXXVII., 1891.

[6] Garnier: Ueber den normalen und pathologischen Zustand der Zonula Zinnii, Archiv f. Augenheilkunde, Bd. XXIV., 1892.

[7] Retzius: Ueber den Bau des Glaskörpers und der Zonula Zinnii in dem Auge der Menschen und einige Thiere, Biologisch. Untersuch., N. F., VI., 1894, S. 84.

[8] Czermak: loc. cit.

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and its expansion over the lens-capsule undergoes absorption, the young zonular fibres alone remaining.

The immature fibres thus formed converge towards the position of the future orbicular zone, where they later become intimately attached to the anterior extension of the hyaloid membrane when that structure appears. Genetically, therefore, the earliest zonular fibres may be regarded as a product of the primitive vitreous connective substance. Subsequent to the limitation of the vitreous mass by the formation of the anterior boundary layer already described, the fibres constituting the zone of Zinn lose their connection with the vitreous tissue and apparently have their exclusive origin from the inner surface of the orbicular zone in the immediate vicinity of the ora serrata.

The last-named structure, according to the recent studies of Schoen,[1] plays a *rôle* of unsuspected importance in the origin of the zonular fibres. This writer describes the ora serrata as differing essentially at various periods of life, since he finds that in early childhood, before the accommodative function is established, the ora serrata, as usually described, is wanting, its place being occupied by a "transition border," within which the visual portion of the retina gradually gives place to the pars ciliaris. In the eye of the young child, therefore, the ora serrata is represented by a smooth line marking the anterior limit of the proper retinal area; microscopical examination, however, shows that this zone is beset with very minute serrations, between six hundred and eight hundred in number, from each of which springs a delicate fibre which takes part in the formation of the zonula.

The macroscopic appearances usually described as the normal condition of the ora serrata, in which about forty well-marked teeth are present, Schoen[2] regards as the result of secondary functional changes induced by the continual pull exerted by the zonular fibres which have their origin in the minute serrations. A second group of zonular fibres, more deeply situated than those derived directly from the ora serrata, originate, according to this author, as extensions of the epithelial cells which constitute the inner layer of the pars ciliaris retinæ. The tall columnar elements of this stratum terminate in delicate fibres which appear as the direct extensions of the protoplasm of the retinal elements. Assuming that the origin of the zonular fibres has been correctly interpreted by Schoen, the zone of Zinn must be regarded as related to the sustentacular retinal tissue and as the specialized extension of the supporting fibres of Müller. Considered in this light, the retinal sheet is not only continued as the epithelium of the pars ciliaris, but is represented as far as the angle of the ciliary body and the lens-capsule by the prolongation of its supporting tissue as the zonular fibres.

[1] Schoen: Der Uebergangssaum der Netzhaut oder die sogenannte Ora serrata, Archiv f. Anat. u. Physiol., 1895.

[2] Schoen: Zonula und Ora serrata, Anatom. Anzeiger, Bd. x., 1895.

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Most observers, however, will be slow to disregard the strong evidence as to the close genetic relations between the zonula and the mesodermic tissue of the early vitreous, as shown by the mode of development of the structures under discussion, and will, therefore, consider the view attributing the origin of the zonular fibres to the retinal tissue as not beyond question.

Depending upon their grouping and course, the zonular fibres in the adult eye may be divided into two varieties, the *chief* and the *accessory*. The *chief zonular fibres*, which include the orbiculo-capsular and ciliocapsular subgroups suggested by Czermak and adopted by Topolanski and by Garnier, constitute the principal bond of union between the crystalline lens and the surrounding ciliary body, and are the chief constituents forming the zonula Zinnii.

Following the classification of Garnier,[1] the chief accessory fibres may be grouped as—1, *Orbiculo-antero-capsular;* 2, *Orbiculo-postero-capsular;* 3, *Cilio-postero-capsular;* 4, *Cilio-equatorial.*

The *orbiculo-postero-capsular fibres* include those occupying the most posterior and internal position and lying in close relation with the anterior boundary layer of the vitreous, without, however, taking origin from the latter. The general relations of the zonular fibres at their origin to the ora serrata and the pars ciliaris retinæ have been subjects of much discussion. Both Iwanoff[2] and Berger[3] regard the fibres as taking origin behind the ora from the vitreous; Schoen[4] upholds that their point of beginning corresponds to the ora serrata itself; Dessauer[5] declares that the fibres never reach the ora serrata; Czermak maintains[6] that they begin shortly in advance of the ora by intra-cellular attachment with the epithelium of the pars ciliaris retinæ; while Topolanski[7] regards their zone of origin as beginning from one to one and a half millimetres in advance of the ora serrata and extending over the entire remaining surface of the ciliary body, including the elevations of the ciliary processes as well as their sides and intervening valleys. These latter conclusions correspond most closely with the results of study of the author's sections.

Regarding the particular fibres in question,—those constituting the orbiculo-postero-capsular group,—it may be accepted that they spring from the prolongation of the hyaloid membrane investing the ciliary ring, the innermost arising almost immediately in front of the ora serrata. The long

[1] Garnier: loc. cit., S. 35.

[2] Iwanoff: Das Glaskörper, Stricker's Handbuch der Lehre von den Geweben, Bd. II., 1872.

[3] Berger: Beiträge zur Anatomie der Zonula Zinnii, Archiv f. Ophthalmol., Bd. XXVIII., 1882.

[4] Schoen: loc. cit.

[5] Dessauer: Zur Zonulafrage, Klinische Monatsblätter f. Augenheilkunde, Bd. XXI., 1883.

[6] Czermak: loc. cit.

[7] Topolanski: loc. cit.

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zonular fibres have, without exception, a meridional course, and when of considerable thickness are resolvable into bundles of delicate fibrillæ. The close association of the posterior fibres with the vitreous impresses upon them a slight convexity, although the general direction of the bands is nearly straight, particularly throughout that part of their course as they pass from the ciliary processes to their insertion in the posterior lens-capsule. When about to join the capsule, the zonular fibres break up into groups of radiating fibrillæ which meet the capsule within an area of local thickening and continue for some distance generally parallel to the surface of the lens, becoming more and more attenuated and finally lost in the substance of the capsule. Retzius[1] regards the minute elevations on the surface of the lens to which the fibrillæ pass as indicative of the presence of a *pericapsular membrane;* in the latter structure he recognizes an external zone of the capsule the differentiation of which is to be referred to initial genetic relations of the vascular mesodermic tissue enclosing the young lens. Czermak and Topolanski have shown that the zonular fibres are more numerous in the very young eye than at any later time, the fibres becoming fewer with the advance in age.

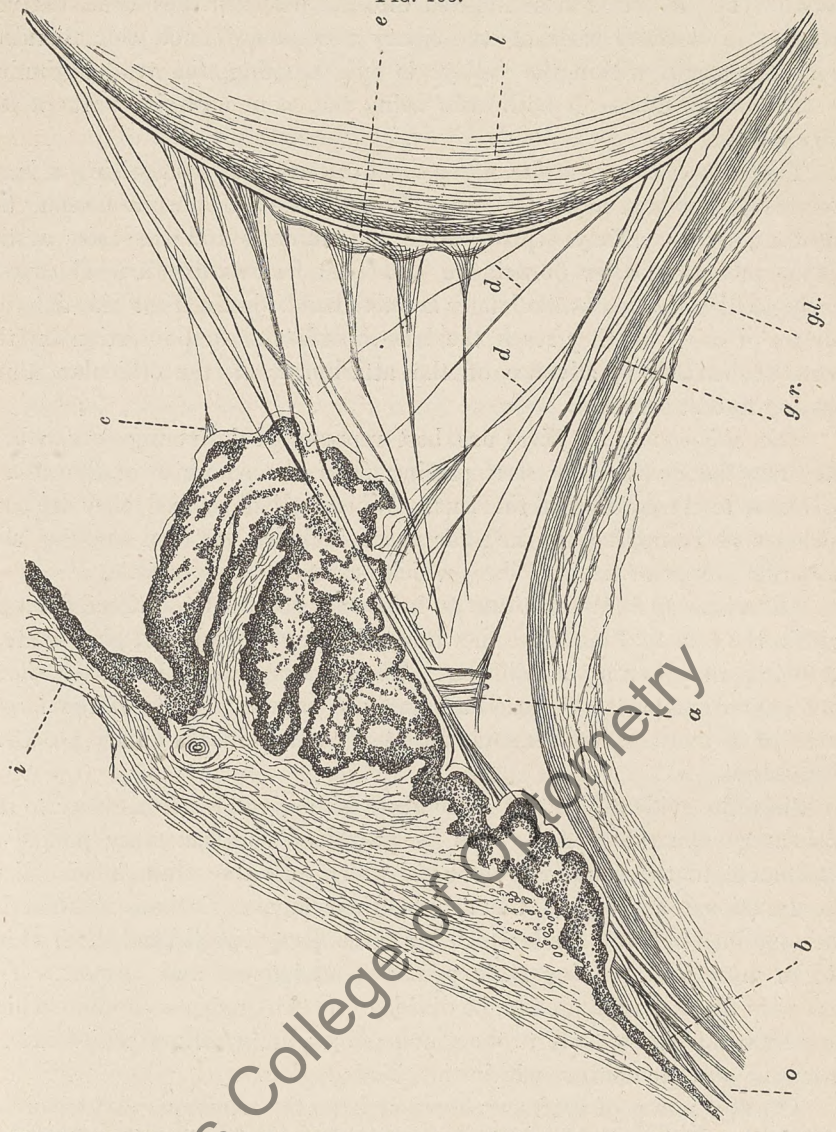
The *orbiculo-antero-capsular fibres,* as indicated by their name, extend from the orbicular region to the anterior surface of the lens-capsule, and constitute the thickest and strongest bands of the zonula. They take origin from the smooth part of the ciliary body behind the processes, and receive numerous accessory fibres throughout their course over the ciliary body. Their relation to the valleys between the ciliary processes is such that they form bundles of considerable size, which are maintained in close union with the sides of the valleys by means of numerous delicate accessory bands. In the posterior part of their course these fibres lie intimately united to the glassy lamella of the ciliary region, the latter membrane occluding the interfibrillar clefts, and thereby producing the appearance of a continuous sheet or membranous zonula, as described by Schwalbe. That the zonula, however, is composed of distinct fibres is shown by careful inspection of surface views of the structures in question. Serial sections passing through the ciliary processes in planes at right angles to the course of the chief zonular fibres are of interest as showing the relation of the fibres to the elevations and valleys. Such preparations show that the fibres are usually associated into bundles of varying size, which, while following the general contour of the depression lodging them, are not closely applied to the adjacent walls, but are separated from them by a more or less conspicuous cleft; the fibres occupying the summit of the process, on the contrary, are usually in intimate relation with the elevations. Retzius, who has furnished a number of careful figures showing the transversely sectioned fibres *in situ*, calls attention to these relations, as well as to the proximity of the posterior group of zonular fibres to the anterior boundary

[1] Retzius: loc. cit., S. 86.

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of the vitreous body, this relation being naturally most marked in the orbicular zone, where the space between the wall of the eyeball and the

FIG. 105.



Meridional section through the ciliary region of an adult human eye. (Retzius.)—*l*, equatorial periphery of lens; *g.l.*, vitreous substance; *g.r.*, anterior boundary of same; *o*, orbicular space; *i*, root of iris; *a*, short, robust attachment-fibres of the posterior zonular trabeculæ; *b*, posterior fibres related to vitreous; *c*, anterior fibres from ciliary processes; *d*, ciliary fibres crossing and adhering to the zonular trabeculæ; *e*, clefts between the pericapsular membrane and the lens-capsule. Low amplification.

vitreous is narrow. The study of incomplete sections of the ciliary body, in which the fibres occupying the valleys are seen passing to the anterior capsule, is misleading in so far that the antero-capsular fibres encountered do

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not take their primary origin from the valleys, as seemingly is the case, but from more posteriorly lying points. The distinction sometimes made, therefore, that the zonular fibres arising within the valleys pass to the anterior capsule, while those inserted into the posterior capsule are derived from more elevated parts of the ciliary processes, is not well founded, since the origin within the valleys is only seeming, the true beginning of the zonular fibres in both cases being the more posterior parts of the ciliary body.

The *cilio-postero-capsular fibres* constitute a group comprising a large number of bands of moderate size. These fibres—according to Garnier the most numerous variety—spring from the summits and the sides of the ciliary processes; after pursuing a somewhat backwardly directed course, during which they cross the longer zonular bands destined for the anterior surface of the lens, they reach the lens-capsule and find insertion on the posterior surface in advance of the attachment of the orbicular fibres passing to that surface.

The *cilio-equatorial fibres* are best represented in young eyes, where they may be occasionally seen passing from the summits of the ciliary processes to the equator of the lens. When well developed, they are conspicuous as occupying the angular space included between anterior and posterior groups of zonular fibres which pass to the lens-capsule.

The accessory fibres constitute an important source of additional strength within the zone of Zinn, since they brace the longer bands and give fixation to their points of ciliary attachment. The accessory fibres are usually short, and pass from parts of the ciliary body to adjacent bands of the larger series or to more or less remotely situated portions of the ciliary processes themselves.

Since the evident object of these fibres is to give greater security to the suspensory apparatus of the lens by providing supplementary points of attachment to the zonular fibres upon which falls the strain incidental to the functional activity of the zonula, their purpose is best attained by the combined effect of bands which brace the fibres directly and those which aid in more firmly fixing their points of attachment and support. The accessory fibres may, therefore, be divided into two groups,—(*a*) those which pass from the ciliary body to the zonular fibres, and (*b*) those which extend from one point to another within the ciliary region.

The first group of accessory fibres includes the numerous short bundles of fibrillæ which unite the orbiculo-capsular fibres with the adjacent surface of the ciliary area, whether they be strands which pass to the long fibres from the orbiculus ciliaris or from the sides and bottoms of the valleys. Since these supporting bands often join the sides of the zonular fibres with considerable obliquity, they serve to brace the fibres against lateral displacement as well as to afford additional security of attachment in the line of the meridional strain.

The second group of accessory fibres embraces the bands having the

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support of the ciliary processes as their particular object. Two sets of such fibres may be recognized,—(*a*) the *orbiculo-ciliary* and (*b*) the *intra-ciliary*. The first of these pass from the orbicular zone to the ciliary processes, and hence prevent the forward displacement of these structures; the second extend between the various parts of the processes themselves, and insure additional security to these elevations by giving greater strength to their lateral walls.

It is evident from the foregoing description of the zone of Zinn that the present conceptions concerning this structure very materially differ from the older views, according to which the zonula represented membranous formations: in contrast to the latter view, it is now recognized that the zonula consists of the interlacement of the several sets of individual fibres already considered in detail, and that the membranous suspensory ligament of the lens as formerly accepted does not exist.

Appreciation of these details must necessarily profoundly influence our conceptions concerning the much-vexed question as to the existence, the character, and the boundaries of the canal of Petit.

The *canal of Petit*, as regarded by the older anatomists, consisted of the annular space, triangular in section, which surrounded the margin of the lens, and was bounded by the last-named structure within and the anterior and posterior lamellæ of the zone of Zinn in front and behind. The correctness of the older classic description of the canal of Petit was conspicuously challenged by Merkel[1] in 1870, since which time the increasing exactness of our knowledge of the true constitution of the zonula has rendered the existence of such a closed perilenticular annular channel less and less tenable. A striking exception to the general tendency of belief was presented by the paper of Aeby,[2] in which this author undertook the energetic defence of the older conception of the canal. Of the modified views concerning the presence of a canal of Petit, that of Schwalbe[3] is noteworthy, since this authority, while denying the splitting of the hyaloid, as formerly accepted, still holds the existence of a closed annular space. According to Schwalbe, the anterior wall of the canal of Petit is formed by the zonula, and its posterior boundary by the anterior surface of the vitreous body.

The more recent investigations concerning the nature of the zonula, as already described, have demonstrated beyond dispute that the long-accepted membranous zonula does not exist, the component fibres in no sense forming a closed canal. In the light of our present knowledge, therefore, the existence of a canal of Petit can no longer be maintained, the space formerly apportioned to the canal being in reality but a part of the posterior chamber. The confines of the latter space, as emphasized by Topolanski, are the lens,

[1] Merkel: Die Zonula ciliaris, Göttingen, 1870.

[2] Aeby: Der Canalis Petiti und die Zonula Zinnii beim Menschen und bei Wirbelthieren, Archiv f. Ophthalmol., Bd. XXVIII., 1882.

[3] Schwalbe: Lehrbuch der Anatomie der Sinnesorgane, 1887, S. 145.

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the iris, the ciliary body, including the orbiculus ciliaris, and the vitreous body, covered by the anterior boundary layer. The free portions of the zonular fibres in their passage to the lens imperfectly separate the posterior chamber into subdivisions, one lying between the iris, the anterior part of the ciliary body, and the anterior bundles of zonular fibres, another between the anterior and posterior zonular fibres, and a third between the posterior fibres and the vitreous body. While such subdivisions are apparent in meridional sections, the fact must not be overlooked that these compartments are freely in communication with one another through the interfascicular clefts of the zonula, and that these divisions in no sense represent isolated portions of the general space of the posterior chamber, and are all filled with the aqueous humor. The same relations apply to the *recessus camerœ posterioris* described by Kuhnt[1] and Schwalbe, which communicates with the general space occupied by the contents of the posterior chamber.

THE AQUEOUS HUMOR.

The aqueous humor and its chamber belong to the anterior tract of the lymphatic system of the eyeball. The aqueous space is subdivided by the iris, the free edge of which rests upon the anterior surface of the lens, into two imperfectly separated compartments, the anterior and the posterior chamber. The latter space is especially related to the production of this lymphatic fluid, since, as already described, the highly vascular ciliary body is the particular structure interested in its secretion.

With the exception of a few leucocytes, the aqueous fluid is without morphological elements. Its chemical composition, as given by Lohmeyer,[2] includes,—

Water	986.87
Solids	13.13
Proteids	1.22
Extractives	4.21
Inorganic salts (sodium chloride, 6.89)	7.70

The proteids, according to Halliburton,[3] are similar to those in other forms of lymph,—namely, fibrinogen, serum-globulin, and serum-albumin. The reducing substance found by Kuhn[4] constantly present in the aqueous humor of the rabbit and the ox resembles sugar, and has been usually assumed as being such; Gruenhagen,[5] however, denies this, on the ground that the substance will not undergo alcoholic fermentation. The

[1] Kuhnt: Ueber einige Altersveränderungen im menschlichen Auge, Sitzungsberichte d. ophthalmolog. Gesellschaft zu Heidelberg, 1881.

[2] Lohmeyer: Quoted in Gorup-Besanez's Lehrbuch d. physiolog. Chemie, 1878.

[3] Halliburton: Text-Book of Chemical Physiology and Pathology, 1891, p. 350.

[4] Kuhn: Zur Chemie des Humor aqueus, Archiv f. d. gesammt. Physiologie, Bd. XLI., 1887.

[5] Gruenhagen: Zur Chemie des Humor aqueus, Archiv f. d. gesammt. Physiologie, Bd. XLIII., 1888.

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same observer reports the presence of minute quantities of urea and sarcolactic acid.

While the entire quantity of aqueous humor is affected by blood-pressure, as shown by Chabbas,[1] the fluid usually present weighs from .23 to .32 gramme, according to the estimates of Jaeger[2] and of Rauber;[3] the specific gravity is 1.0053, and the index of refraction about 1.337. Compared with that of the vitreous body, the refractive power of the aqueous humor shows a slight increase, being below that of the cornea, and, of course, distinctly less than the exponent of the lens. According to the experiments of Krause,[4] Fleischer,[5] Hirschberg,[6] and Aubert,[7] the indices of refraction of the eye-media are, approximately, cornea 1.360, aqueous humor 1.337, crystalline lens 1.425, vitreous body 1.336, when the refractive index of distilled water is 1.334. All parts of the posterior chamber, including the intra-ciliary recesses and the intra-zonular spaces, are filled with the aqueous humor; the latter fluid penetrates into the anterior chamber through the pupillary opening by means of the capillary cleft which usually exists between the anterior surface of the lens and the edge of the iris. The important *rôle* continually played by the spaces of Fontana and the adjacent spongy tissues in effecting the escape of the aqueous fluid from the anterior chamber into the annular sinus of Schlemm and the associated anterior ciliary veins has already been considered; it is here only necessary to recall the existence of this arrangement, which is so essential in maintaining the equilibrium of intra-ocular tension by permitting the exit of the lymph-fluid which collects within the anterior segment of the eyeball.

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[1] Chabbas: Ueber die Secretion des Humor aqueus in Bezug auf die Frage nach den Ursachen der Lymphbildung, Archiv f. d. gesammt. Physiologie, Bd. XVI., 1878.

[2] Jaeger: Ueber die Einstellungen des dioptrischen Apparatus im menschlichen Auge, 1861, S. 14.

[3] Rauber: Lehrbuch des Menschen, 4te Aufl., Bd. II., 1894, S. 725.

[4] Krause: Die Brechungsindices der durchsichtigen Medien des menschlichen Auges, 1855.

[5] Fleischer: Neue Bestimmungen der Brechungsexponenten der durchsichtigen flüssigen Medien des Auges, 1872.

[6] Hirschberg: Ueber Bestimmung der Brechungsindices der flüssigen Medien des menschlichen Auges, Centralblatt f. d. medicin. Wissenschaften, No. 13, 1874.

[7] Aubert: Physiologische Optik, Graefe u. Saemisch's Handbuch d. gesammten Augenheilkunde, Bd. II., 1876.

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ANATOMY OF THE INTRA-CRANIAL PORTION OF THE VISUAL APPARATUS.

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INTRODUCTION.

It is impossible to study the structure of the brain as a subject by itself. Only when considered as a part of the sciences of embryology, comparative anatomy, and physiology does it become intelligible. The cutting and staining of sections in series have been brought to such perfection within the last few years that those who are not experts in the subject are tempted to imagine that anatomists have at their disposal methods which will enable them to solve all questions as to the mutual relations of the fibres, cells, and plexus of which the central nervous system is composed. Nothing could be further from the truth, for the facts of which we are able to make use in our attempts to picture to ourselves the machine in action are discovered from a study of its development, its variations in animals variously endowed, its reaction to stimulation, and its degeneration after localized disease, rather than through any strictly anatomical investigations. It is impossible to study the anatomy of the central nervous system apart from its physiology, or its physiology apart from its pathology. Neurology is a study to which all other sciences contribute; it is not a branch of any other science.

If it be true that even the structure of the nervous system as a whole cannot be treated as a separate subject standing on its own basis of anatomical observations, no argument will be needed to prove that the study of a part of the system, such as the cerebral mechanism of vision, cannot be detached from the study of the whole. It must be viewed in the first place in its relation to other subjects.

The Ontology of the Nervous System.—The earliest changes in the embryo are associated with the formation of the nervous system. As soon as the blastoderm is formed, its dorsal layer, or epiblast, begins to be lifted up in two ridges which border a longitudinal groove. The ridges continue to grow until they meet in the mid-dorsal line and thus enclose a canal, the canal of the spinal cord, and its anterior dilatations, the ventricles of the brain. The walls of this canal develop into the central nervous system; its cells give off processes which run towards the periphery as the anterior

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roots of the nerves. The posterior roots of spinal nerves and the sensory cranial nerves are not developed as outgrowths from this neuro-epithelial tube, but as ingrowths from a series of rudiments lying on either side of the tube, the rudiments of spinal ganglia and their homologues within the cranium. These rudiments are also of epiblastic origin, and therefore the whole nervous system is developed from tissue which elsewhere becomes the skin.

Histogeny.—The neuro-epithelial cells which enter into the formation of the nervous system very early show a distinction into two sets,—viz., (*a*) the germ-cells, which retain their power of subdivision, as indicated by their abundant protoplasm and large nuclei with conspicuous chromatin-skeins; and (*b*) the spongioblasts, of which the bases rest against the central canal, while their bodies are elongated until they not only traverse the whole thickness of the spinal cord, but also give off, near its periphery, lateral processes which enter into the formation of a reticulum, the *velum confine.* The germ-cells (*a*) retain their situation close beneath the lining epithelium of the central canal, where the mitotic figures of their nuclei make them conspicuous in any stained section; the cells to which by their subdivision they give rise take up their positions farther outward in the gray matter, as neuroblasts. The neuroblast becomes a nerve-cell; its undivided process a nerve. The process may run out of the cerebro-spinal axis as a peripheral nerve, or up or down within the reticulum of the velum confine as a longer or shorter intra-axial commissural fibre.

The Phylogeny of the Central Nervous System.—Opinions differ as to the condition among existing animals which we may look upon as representing the primitive or original form of the nerve-elements, but it is generally allowed that we have to regard nerve-fibres as filaments which came into existence for the purpose of uniting contractile cells with the sensory cells of the surface, the stimulation of which rendered contraction desirable. Thus, the first compound animal was a hollow sphere of cells. This, being "pitted in," became a gastrula, or animal with a stomach-cavity lined by endoderm and with an outer wall of ectoderm. The ectodermal or epithelial cells developed contractile processes, and, as these processes increased in size and importance and began to assume the properties of independent muscle-cells, constituting a third layer (mesoderm) in the animal's body wall, the conducting strand which united each muscle-fibre to an ectodermal cell was drawn out into a nerve-fibre. At this stage the animal was only capable of answering to general stimulation of its surface by a universal contraction.

The origin of sense-organs is to be traced to the fact that certain spots on the surface which, owing to their favorable situation or to chemical differentiations which gave rise to pigment, crystals, or other substances, were rendered particularly liable to stimulation, became the organs from which information of danger was most frequently transmitted to the muscle-fibres by whose contraction the danger was escaped. These sensitive spots were the first sense-organs.

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So long, however, as the sense-organs retained their connection with certain groups of muscle-fibres only, their usefulness must have remained extremely small. The next step in advance, and one which seems to have occurred with great rapidity, was the introduction of a distributive mechanism at the base of each sense-organ, by means of which it was placed in connection with various parts of the contractile sheet of mesoderm. There can be very little doubt that this commencement of a nervous system was effected by the deposition of certain of the cells of the primitive sense-organs, from their posts as scouts, and their utilization for the purpose of establishing communications between the cells which remained on the surface and the contractile cells. It is possible in the covered-eyed Medusidæ (the larger jelly-fishes) to find, only just beneath the surface, cells intermediate in form between sensory cells and ordinary nerve-cells.

Formation of a Central Nervous System.—The efficiency of these groups of "distributive cells" was soon increased by their union, by means of commissural fibres, into a central nervous system. This stage in the development of the system can be seen in the naked-eyed Medusidæ. The margin of the swimming-bell of Sarsia carries two such nerve-rings, the lower rich in cells. With the acquisition of this ring we find that the animal becomes able to localize any spot on its bell which may be injured; it swings its polypite to the injured spot and performs other simple reflex actions.

For the purposes of the present article it is most important to remember that the sense-organs are segmental, and that the rudiments of the central nervous system were laid down about the bases of these organs. As we ascend the animal scale we find centralization carried farther and still farther, but we have every reason for believing that the spinal ganglia, which are formed by delamination of the epiblast and not from the neuro-epithelial tube, are the remains of the groups of cells which were submerged in the mesoderm beneath the primitive sense-organs. Save these large bipolar cells, which give off one process towards the periphery and another towards the spinal cord, all nervous elements have been withdrawn, from the vicinity of the greater number of the sense-organs, to a more central and sheltered situation. The centralization of the gray matter originally laid down at the base of the ear, the nose, and the eye is not, however, carried to anything like the same extent as in the case of the other sense-organs. The bipolar cells of the ganglion spirale are still to be found in the vicinity of the cochlea. The olfactory bulb contains granules, plexus, "gelatinous substance," and nerve-cells, which in segments farther back are all, save the granules (bipolar cells), withdrawn into the cerebro-spinal axis.

The retina is more primitive in plan of structure than either the nose or the ear; for its several layers, beneath its epithelial cells and their nuclei (outer nuclear layer) and in immediate juxtaposition with them, consist of granules (bipolar cells), plexus (molecular layer), and nerve-cells arranged in regular strata. Granules, cells of ganglion spirale and cells of spinal ganglia, molecular layer of retina, stratum gelatinosum of olfactory bulb, and sub-

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stantia gelatinosa Rolandi of the spinal cord are, as we believe and have taught for the last ten years,[1] strictly homologous. It is essential that this fact should be recognized before we attempt to trace the connections of the optic nerve with the brain. As a sense-organ the eye probably assumed its permanent and immutable form before the formation of the central nervous system was carried very far. The nervous elements at its base have never been withdrawn into the spinal cord, but retain their local situation in the retina. Before we try to trace the course of the optic tract within the brain we must disabuse our minds of the idea that its connections will be found to be arranged upon the same plan as those of other sensory nerves or posterior roots. All other sensory roots enter into intimate relations with the substantia gelatinosa Rolandi. The portion of this substance which belongs to the optic nerve lies in the retina. After the posterior roots have undergone arborization in the central gray matter of the spinal cord, multipolar cells collect the impulses which the roots have delivered and transmit them by their axis-cylinder processes to higher regions of the cord or brain. Such *collecting cells*, also, are to be found in the retina, and there is no analogy in other nerves from which we can judge as to the nerve-tissue in which we ought to expect that the axis-cylinder processes of these collecting cells will end.

The cerebral connections of the retina must be treated as a problem by itself. We must be careful not to infer that the connections of the optic fibres will follow any plan which we find to hold good for other sensory nerves.

In the evolution of its cerebral mechanism the optic nerve stands almost alone. The phylogeny of the brain is far from being understood, but there are certain conclusions which we are fully justified in drawing from the study of its typical form in the several classes of vertebrates. In fishes the cerebrum is very small and the rhinencephalon distinct from the rest of this organ. The optic lobes are large and distinctly cortical in plan of formation, and we find in addition trigeminal and vagal lobes of certain dimensions. The optic lobes are just as large in birds and reptiles, but the other lobes have almost disappeared. The cortex cerebri, which is responsible for the immense development of the human brain, is practically absent in fishes and birds and only makes its appearance in an unmistakable form in reptiles. It seems impossible to avoid the conclusion that each segment of the vertebrate brain was at one time complete in itself, autonomous, carrying on all the traffic brought to it by the nerve with which it was especially connected, whether it were the olfactory, optic, trigeminal, or vagus.

In fishes, amphibians, reptiles, and birds the chief cerebral connection of the optic nerve is with the optic lobe (corpus bigeminum). The large

[1] Hunterian Lectures, Royal College of Surgeons, 1885–86; British Medical Journal, March, 1885, and March, 1886.

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size and complicated structure of this body show that it suffices for the elaboration and reflection of all visual impulses. In the lower mammals the corpora quadrigemina are still of large size relatively to the rest of the brain. Their minute structure shows that they carry on important work. As the mammalian scale is ascended the corpora quadrigemina become progressively smaller and poorer in gray matter, until in the Primates they form but a very small proportion of the whole brain. It is true that the proportion between their weight and the body-weight is not greatly changed, and it might be argued that they still retain the functions which they first came into existence to perform; but their impoverishment in nerve-cells, considered in connection with the diversion to the fore-brain of a great number of the optic fibres which are distributed to the mid-brain in lower animals, indicates in an unmistakable manner, as we think, that the human cortex cerebri has assumed functions originally performed by other parts of the brain.

COURSE OF THE OPTIC NERVES.

The course and connections of the optic fibres have been worked out chiefly in the human brain, and especially by means of pathological investigations. It is convenient, therefore, that our description of these tracts in their minute subdivisions should have reference to man.

Optic Nerve.—This nerve has a length of about five centimetres, of which three centimetres lie within the orbit, one centimetre is within the optic canal, and one centimetre is intra-cranial. Within the eyeball its fibres are non-medullated. They acquire their myelin-sheaths immediately after traversing the sclerotic, and hence the nerve appears constricted as it leaves the eyeball. Beyond this point the nerve is a firm, round, white cord five millimetres in diameter, its cross-section being nine square millimetres, of which area four square millimetres must be deducted for connective tissue. Its fibres are collected into fasciculi very much after the manner of an ordinary peripheral nerve, although the septa of connective tissue, rich in nuclei, which enter from the periphery are less regular in thickness and in disposition than ordinary endoneurium. The nerve contains, according to Salzer's enumeration,[1] about four hundred and thirty-eight thousand medullated fibres, of extreme tenuity. Such an enumeration must, however, be received with caution, owing to the obvious difficulty which the counting of very minute fibres presents; it is difficult, perhaps impossible, to recognize all the smaller fibres, and certainly impossible to count them in any section.

Krause[2] describes the measurable medullated fibres as varying in size from 0.001 to 0.014 of a millimetre, the most numerous being those of 0.006 of a millimetre. He considers that Salzer has counted these fibres

[1] Sitzungsberichte der k. Akad. der Wissensch. zu Wien, Math. naturw. Klasse, Bd. lxxxi., Abth. iii. p. 7.

[2] Archiv f. Ophthalmologie, xxvi., Abth. I. p. 102.

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accurately, but has omitted from his reckoning all the finest fibres (of about 0.0005 of a millimetre), which are at least as numerous as the fibres which he counted, bringing the total number up to about one million.

Von Gudden divided the fibres into two classes, large and small; but he did not doubt that both were afferent, although he surmised that while the large fibres carried visual impulses the small might very probably be devoted to the mechanism for carrying out the pupil-reflex. Von Monakow[1] makes a further use of the difference in size, for he conjectures that the two classes of fibres belong to two distinct systems,—(*a*) the large fibres, which originate, he thinks, in the large nerve-cells of the retina and grow centripetally into the reticulum of the external geniculate body and the pulvinar of the optic thalamus, and (*b*) the fibres of small calibre, which originate in the cells of the superficial gray matter of the corpora quadrigemina and grow outward to terminate in the inner nuclear layer of the retina.

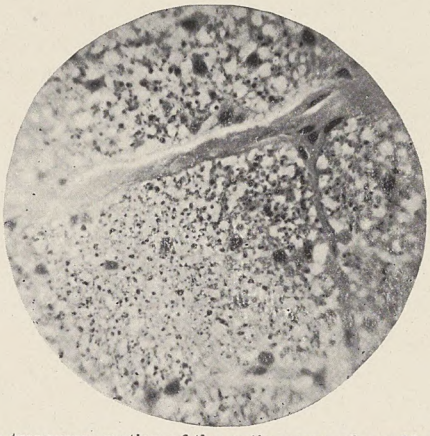
However probable such a division into smaller centrifugal and larger centripetal fibres may be, it would be premature as yet to regard it as definitely proved. There can be no doubt as to the existence of larger and smaller fibres (Fig. 1), but we agree with Krause in thinking that the fibres are not sufficiently uniform in diameter to allow of arrangement in two classes. We estimate that there are on the average about eight smaller fibres of various categories to each distinctly large fibre, but we have as yet failed to follow the two classes to their destination in the brain or to correlate the difference in size with difference in function. A glance at the photograph reproduced in Fig. 1 suggested that the smaller fibres might be ultimately connected with rods, the larger with cones; but this is not the case, for the distinction in size is as well marked in animals which have cones only (*e.g.*, the alligator or the turkey) as in mammals. Nor is Von Monakow's supposition as to their mode of growth and cerebral destination supported by an examination of the optic tract above its division into external and internal roots, since throughout both roots of the tract the large fibres are scattered about among the small, just as they are in the optic nerve. The only definite observations upon the direction of growth of the fibres[2] with which we are acquainted show us the fibres growing inward from the retina, although it is quite possible that these fibres are the first to grow and that centrifugal fibres appear later. The complete ascending degeneration which follows enucleation of the eyeball points to the centripetal growth of all the fibres; Von Gudden, Henschen, and others, however, have observed descending degeneration as a consequence of destruction, experimental or pathological, of the optic tract. It is of fundamental importance that we should obtain exact information as to the number, size, and character of the optic fibres, their direction of growth,

[1] Archiv für Psychiatrie, vol. xx. p. 780.

[2] Froriep, Anat. Anzeiger, 1891, vi. 6, p. 155.

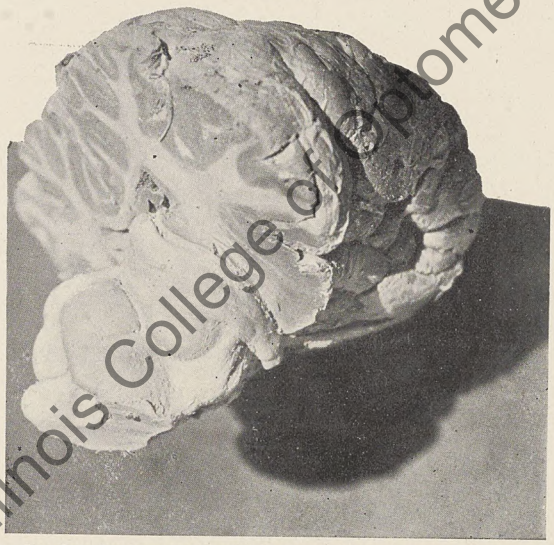
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FIG. 1.



Photomicrograph of a transverse section of the optic nerve of a calf, magnified 700 diameters. The section shows trabeculæ of connective tissue, connective-tissue nuclei (the large dots), and, much smaller than the latter, the axis-cylinders of optic nerve fibres. Of the nerve-fibres a certain number are larger and tend to lie in free spaces, but the majority are extremely minute, more or less collected into groups, and not surrounded by free spaces. The section was stained in carmine.

FIG. 6.



Mid-brain of ox, showing the manner in which the optic tract grasps the back of the thalamus and surrounds the geniculate bodies. Behind the internal geniculate body the optic tract appears to give a bundle to the crus cerebri.

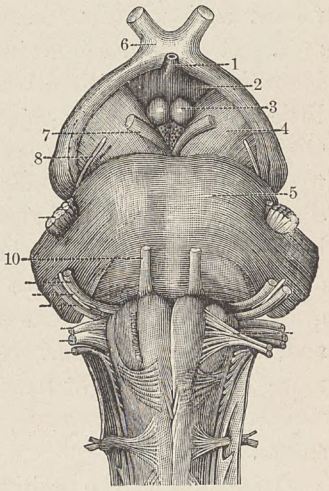
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and their retinal and cerebral connections; but the answers given as yet to these questions are, unfortunately, little more than speculations.

Optic Chiasm.—The round optic nerves meet beneath the floor of the third ventricle to form the transversely disposed and somewhat flattened optic chiasm or commissure. (Fig. 2, *6*.) The chiasm is lodged in a recess in the thin wall of the 'tween-brain in front of the tuber cinereum, and forms a part of its floor. Owing to this continuity of the floor of the ventricle and the optic chiasm, advantage is taken of the situation of the latter by certain other commissural fibres which do not belong to the optic apparatus, —namely, the commissures of Meynert and Van Gudden. Apart from such accessory tracts the chiasm consists of two sets of fibres,—the crossing fibres, from the nasal sides of the two retinæ, which occupy its centre, and the uncrossed fibres, from the temporal sides of the retinæ, which constitute its lateral portions. The fibres which originate in the macula lutea have in recent years been traced with such precision as almost to merit separation into a third class or system, the "maculary fascicle," although they share with the other optic fibres the division into uncrossed fibres of the temporal side and crossed fibres of the nasal side of the retina. In a number of cases of central scotoma,[1] for the most part of toxic origin, this maculary fascicle has alone degenerated, and, although it cannot be distinguished as a separate bundle in a healthy nerve, it is found when degenerated to occupy at first the outer and inferior portion of the optic nerve, gradually withdrawing to its centre, so that when it enters the chiasm it and the fascicle of the opposite side lie symmetrically in the two foci of the ellipse. In the chiasm it divides into a nasal portion, which decussates with its fellow in the centre of the chiasm, and a lateral uncrossed portion, which continues its course into the optic tract of the same side. In the tract the two bundles apparently reunite to form a single bundle in its centre. This theory of the double constitution of the chiasm, of crossed and uncrossed fibres, now almost universally held,

FIG. 2.



The base of the brain.—1, infundibulum; 2, tuber cinereum; 3, corpus albicans; 4, crus cerebri; 5, pons varolii; 6, optic chiasm; 7, oculomotor nerve; 8, fourth nerve (to superior oblique muscle of the eyeball); 10, sixth nerve (to external rectus muscle of the eyeball).

[1] Leber, Archiv für Ophthalmologie, xv. p. 67; Samelsohn, Archiv für Ophthalmologie, xxviii., 1, p. 1; Nettleship, Transactions of the Ophthalmological Society, i.; Vossius, Archiv für Ophthalmologie, xxviii., 3, p. 201; Bunge, Gesichtsfeld und Faserverlauf in optischen Leitungsapparat, Halle, 1884; Uhthoff, Archiv für Ophthalmologie, xxxii., 3, p. 95; Thomson, Archiv für Psychiatrie, xiii. p. 352.

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was formulated by Newton[1] as an hypothesis accounting for stereoscopic vision. Since it is not accepted by all anatomists, however, it is well that we should examine the evidence upon which this theory is based, and the arguments which may be urged against it.

Looking at the subject first of all from the physiological side, it will be seen that the division of each retina into two parts, of which one is united with the brain by crossed fibres and the other by uncrossed fibres, allows of the connection of two "corresponding retinal points" with a single cortical area. It is almost impossible to conceive of a cerebral mechanism of binocular vision arranged upon any other plan. Human beings pay very little attention to any objects which are not seen by both eyes at once. Objects situate near the periphery of the field of vision which are brought to a focus on one retina only are perceived by most people merely as vague differences of light and shade. In all fishes and birds and in many members of each of the other classes of vertebrates in which the eyes are placed on the side of the head, we must suppose that the conditions of sight are quite different. In them each field of vision is independent of the other, and, although there may very probably be a part of each retina which is more sensitive to light than the rest, the visual fields do not overlap, but form a continuous expanse, each object giving rise to an independent sensation.

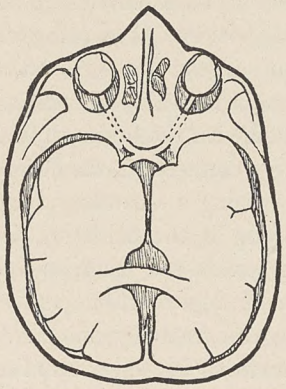
In comparing the position of the eyeballs in various animals we must not be misled by the direction of the optic nerve, which, in order that the blind spot may not fall in the optic axis, enters the retina on the inner side of the globe; nor is it necessary that we should have regard only to the axis about which the refractive media of the eye are centred, since in man, as in most animals, the sensitive screen is continued farther on the nasal than on the temporal side of the globe; but for the purposes of this article—namely, the tracing of retinal fibres to the brain—we may consider the position of the retinal screen as a whole. In a man the axes which bisect the central points of the retinæ would meet if prolonged backward at an angle of less than 45° (Fig. 3); in a dog, at an angle of about 90°; in a horse, at an angle of about 135°; in a rabbit (Fig. 4) they lie almost in the same

[1] "Are not the species of objects seen with both eyes united where the optic nerves meet before they come into the brain, the fibres on the right side of both nerves uniting there, and after union going thence into the brain in the nerve which is on the right side of the head, and the fibres on the left side of both nerves uniting in the same place, and after union going into the brain in the nerve which is on the left side of the head, and these two nerves meeting in the brain in such a manner that their fibres make but one entire species or picture, half of which on the right side of the sensorium comes from the right side of both eyes through the right side of both optic nerves to the place where the nerves meet, and from thence on the right side of the head into the brain, and the other half on the left side of the sensorium comes in like manner from the left side of both eyes? For the optic nerves of such animals as look the same way with both eyes (as of men, dogs, sheep, oxen, etc.) meet before they come into the brain, but the optic nerves of such animals as do not look the same way with both eyes (as of fishes and of the chameleon) do not meet, if I am rightly informed."—*Newton's Optics*, *Qu.* 15.

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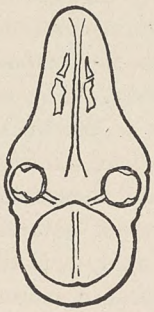
straight line; and it is clear that the more nearly the axes are parallel with one another the more extensively do the fields of vision overlap. The field

FIG. 3.



Tracing from a frozen section of the head of a man, to show the position of the eyeballs.

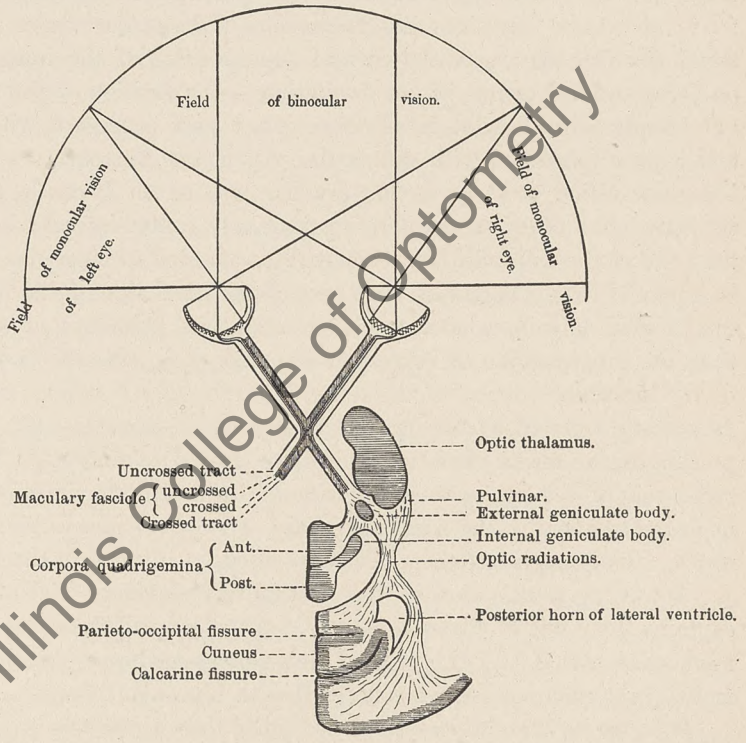
FIG. 4.



Tracing from a frozen section of the head of a rabbit.

of vision for each eye in man (Fig. 5) subtends an angle of about 135°; the combined field of vision embraces, in the horizontal plane, a semicircle.

FIG. 5.



Hence the field of stereoscopic vision, or region in which the visual fields of the two eyes overlap, subtends an angle of about 90°.

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In man, therefore, and in certain monkeys which agree with him in having the eyes directed forward, each retina is divided by a vertical line into a lateral or temporal portion (about three-fourths of the whole), which is concerned with binocular vision, and a mesial or nasal portion (about one-fourth), which can be used only for monocular vision. According to Newton's theory of the construction of the chiasm, all the fibres from the nasal sides of the retinæ cross to the opposite side of the brain, whereas some of the fibres from the temporal sides are connected with the brain on their own side of the body. The crossed is the primitive connection, the diversion of certain fibres to the brain on the same side being a secondary adaptation which keeps pace exactly with the overlapping of the fields of vision, or development of stereoscopy. The size of the uncrossed tract, as traced by observing cases of natural or surgically induced degeneration (and we may say at once that it is impossible to follow the tract by any anatomical method, whether of maceration, teasing, or sections in the coronal or horizontal planes), should, according to this theory, vary directly as the development of binocular vision in the animal, and this we find to be the case. In the rabbit it is so small that it was for a long time overlooked; in dogs it is much larger; in monkeys it is larger still.

In order, however, that the anatomical facts which have been ascertained from a study of the degeneration of fibres through the chiasm should enable us to picture to ourselves the mechanism of binocular vision,—to understand what we may term the mental superposition of the images focussed on corresponding points of the two retinæ,—the division of the retina must not simply coincide with its division into a part concerned with binocular and a part concerned with monocular vision, but the part concerned with binocular vision must be further divided into two. It can be proved that the connection of eye and brain is primitively contra-lateral; it is assumed that the connection with the same side is adapted to binocular vision. It is supposed that, whereas all that part of the nasal side of the retina which can be used only in monocular vision retains its primitive crossed connection, the superposition of corresponding images is effected by the division of the binocular portion of the retina into two halves about a vertical line. Impulses generated by the impact of light upon the temporal side of this portion of the retina of the right eye are carried by uncrossed fibres to the right side of the brain, to which side of the brain the impulses simultaneously generated in the nasal side of the left eye are also carried by crossed fibres. The images are therefore superposed, as it were, in the brain.

According to this view of the cerebral mechanism of vision, the chiasm contains three sets of fibres,—namely, (a) the crossed fibres concerned with monocular vision, (b_1) the crossed fibres concerned with binocular vision, and (b_2) the uncrossed fibres concerned with binocular vision.

It is, we believe, impossible to recognize these three sets of fibres in the optic nerve by any anatomical difference of size or grouping. The observation of the degeneration which results in various animals from enucleation

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of the eyeball does, however, confirm the physiological hypothesis, for the size of the uncrossed tract keeps pace with the development of stereoscopic vision. In the rabbit the bundle of fibres which degenerates in the optic tract of the same side is so small as to be easily overlooked, and its supposed absence is cited, by those who believe in the total decussation of the optic nerves in the chiasm, as a proof of their theory; but it must be remembered that in the rabbit binocular vision is limited to very small portions of the retinæ on their temporal sides, and therefore the uncrossed fibres which belong to half only of the stereoscopic portion of each retina are but a small fraction of the total number of optic fibres. Stereoscopy varies greatly in development in different breeds of dog. It is not surprising, therefore, to find that observers differ widely in their estimate of the size of the uncrossed bundle in this animal. In man stereoscopic vision reaches a high state of development, although, owing to the prominence of the bridge of the nose, it probably does not take such complete possession of the retina as it does in the monkey, and we have now a numerous series of pathological observations which show that in man the direct bundle is of considerable size, and that it occupies the external part of the optic nerve and chiasm.

Most of the cases which have been recorded of disturbance of vision due to cerebral disease were complicated by the coexistence of cortical lesion, but certain cases in which lesion was limited to the optic nerves and tracts have been recorded. One such case in which disease affected the optic nerve of one side and the optic tract of the opposite side would appear to be absolutely conclusive, since the patient retained his sight only for the nasal half of the eye with the sound optic nerve, the limit of the field of vision passing accurately through the fixation point.[1]

The view that the optic nerve is divided in the chiasm into crossed and uncrossed portions is, moreover, supported by Von Gudden's and Ganser's observations of the degeneration which follows enucleation of the eyeball in the adult animal, as well as by the observations of the former with regard to the arrest of development which results when the eyeball is removed at birth.

It does not necessarily follow, however, that the object of this partial crossing is to render stereoscopic vision possible by the "superposition of images in the brain" after the manner we have described at some length. Indeed, certain clinicians, for the sake of explaining cases in which disease of one occipital lobe has seemed to produce crossed amblyopia, have propounded schemes showing the direct bundle as crossing to the opposite hemisphere in the corpora quadrigemina; they regard the right optic nerve as connected solely with the left hemisphere of the brain, its fibres reaching this hemisphere in two groups, one of which crosses in the chiasm, the other in the corpora quadrigemina. Anatomy is, on the whole, opposed to such

[1] Nettleship, Transactions of the Ophthalmological Society, October, 1883.

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an arrangement, although it cannot be asserted that it is impossible. The ultimate settlement of this question must rest with the pathologists. Looking at the matter, however, from the point of view of a comparative anatomist, we think that we may urge very strongly that the evidence before us supports the simple and practical view that the primitive crossed connection of the optic nerves with the brain has been disturbed by the diversion of certain fibres to the same side of the brain in number proportional to the area of retina used in binocular vision, and for the purpose of facilitating stereoscopy.

ORIGIN OF THE OPTIC NERVES.

The anatomy of a large nerve is the anatomy of the separate fibres of which it is composed. It is now almost universally allowed that the axis-cylinder of a nerve-fibre is the process of a nerve-cell. To the cell from which it grew it looks for its nutrition. Cell and fibre must therefore be regarded as a nerve-element or "neuron." The cell gives rise to a number of branching processes in addition to its unbranched nerve-fibre, but whether these "protoplasmic" processes are to be regarded as nervous, in the sense that they distribute nerve-currents, or whether they are simply the roots by which the cell sucks up its nutriment, as Golgi and his followers believe, is a question under discussion. At its distal end the nerve-fibre breaks up into a brush, the twigs of which are very generally, if not invariably, connected with minute bipolar cells or "granules," but whether these granules are to be regarded as belonging to the neuron or as separate elements is at present uncertain. Certain it is, however, that the nervous system is made up of innumerable neurons. The cell of the neuron may lie within the central nervous system, in a spinal ganglion, or, as in the case of the retina, at the periphery, in immediate contact with the sensory epithelium. Each bipolar cell of a spinal ganglion sends one process into the gray matter of the spinal cord and another to the periphery. Each multipolar cell of the anterior horn sends a process to a voluntary muscle, which divides into several branches, each branch ending on a muscle-fibre in a brush of granule-bearing twigs. The other neurons of the central nervous system are placed with their cells in the cerebro-spinal axis, their processes branching in the cortex of the cerebellum or cerebrum, their cells in the cortex and their processes ending in the axis, or with both cells and processes confined to the one or the other of these fields.

Are the fibres of the optic nerve and tract processes of cells which lie in the brain as well as of cells which lie in the retina? While inclined to answer this question in the affirmative, we need, as already hinted, additional evidence.

In what parts of the brain do the processes of the retinal cells branch? The cell-processes may be divided into two groups,—(A) the fibres connected with the fore-brain and (B) the fibres connected with the mid-brain. It may be that all the processes of the retinal cells end in the fore-brain, while the fibres connected with the mid-brain are the processes of cells

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which lie in that region (as Von Monakow believes) and have their terminal arborization in the retina. Von Monakow thinks that the mid-brain fibres are distinguished from the fore-brain fibres by their smaller size. On the other hand, fibres have been observed, it is said, to arise in the cells of the external geniculate body and to take their course into the optic tract,[1] a mode of connection which would certainly lead us to look for their terminal arborizations in the retina; whereas the direct origin of fibres in the mid-brain has not, as yet, been seen. Certain anatomists consider the distinction into large fibres, afferent to the fore-brain from retinal cells, and small fibres, efferent from the mid-brain to the retina, as definitely proved; others describe and figure afferent and efferent fibres as connecting both fore-brain and mid-brain with the retina. Further research is, however, greatly needed, and it is well, at present, to suspend judgment on this fundamental point.

Let us consider Group A first. They may be divided into three, perhaps four, classes,—(*a*) the fibres which enter the external geniculate body, (*b*) the fibres which end in the pulvinar, (*c*) the fibres which pass on to the thalamus, and (*d*) the fibres, if any, which take up their position in the back of the internal capsule and continue their course, without cell-interruption, to the cortex of the brain.

Unfortunately, our information with regard to the exact mode of termination of all these groups of fibres is almost nil.

(*a*) *The Corpus Geniculatum Laterale.*—This is a dense mass of gray matter of very irregular form, indistinctly split into strata by the plates of optic fibres which traverse it. From its anterior surface tongues of gray matter project into the substance of the thalamus, from which they are conspicuously distinguished by their denser ground-substance. The cells of the external geniculate body are variable in size, but smaller than those of the thalamus (10–20 μ, Henle), more angular, and formed of a denser protoplasm. The external geniculate body shrinks both when the eyeball is destroyed and when the occipital lobe is removed or diseased, but how far this shrinking is due to atrophy of the plates of optic fibres which traverse the body and how far it is really due to an alteration in the essential part of the geniculate body—its gray nucleus—is a matter which needs further investigation.

It is asserted by Von Monakow[2] that the ground-substance of this body tends to disappear after removal of the eyeball, while its cells are not affected. If this be true, the geniculate body receives the ascending processes of retinal cells, and does not give origin to the descending fibres of the optic nerve as Bernheimer supposes.

(*b*), (*c*). *The Optic Thalamus.*—No adequate description of the anatomy of this great mass of gray matter has yet been written. It is easy to point

[1] Bernheimer, Sehnerven-wurzeln des Menschen, Wiesbaden, 1891.
[2] Archiv für Psychiatrie, vol. xx. p. 780.

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out that its cells are large (about 40 μ), soft, very liable to break down and disappear in specimens of tissue hardened in the ordinary way, and loaded with yellow pigment; its ground-substance is somewhat loose, light in color, and traversed by innumerable minute nerve-fibres; but we know very little as to the connections of the cells and fibres.

The thalamus is covered by a sheet of white fibres, its stratum zonale, about three-fourths of a millimetre thick. In part, at any rate, the stratum zonale consists of fibres of the optic tract which pass over the external geniculate body, but it also receives fibres from the pedunculus conarii as well as from the sagittal medullary strata of the cerebral hemisphere. It is impossible to unravel this tangle. Nor can we even say how much of the stratum zonale or of the thalamus itself belongs to the cerebral mechanism of vision in the mole. The thalamus is still of considerable size, although smaller than in animals which see. In whales and other aquatic mammals which are destitute of the sense of smell it is short but broad and large. While, therefore, it probably contains the primary centres of the first and second nerves,—the structure of the centres being modified by the presence in the retina and olfactory bulb of much gray matter, included in the case of other peripheral nerves within the cerebro-spinal axis,—the mass of the thalamus may have functions unconnected with either sight or smell.

The pulvinar is the only part of the thalamus which has been shown to atrophy as the consequence of destruction either of the optic nerve or of the occipital cortex. Whatever, therefore, may be the function of the remainder of the thalamus, we are justified in regarding the pulvinar, as well as the external geniculate body, as a primary centre of the optic nerve, and we are probably right in believing that the fibres of the tract which are distributed to these nuclei end by branching in their ground-substance, while fibres for the cerebral cortex take origin in their cells.

The external geniculate body and the pulvinar contain the end-brushes of the retino-thalamic neurons, the cells of the thalamo-cortical neurons. Von Monakow[1] has ascertained that when the occipital cortex is destroyed in new-born animals, the cells of the external geniculate body and the cells and ground-substance of the pulvinar atrophy instead of developing as the animal grows. Certain qualifications as to the parts of these gray masses which atrophy, and as to the amount of the atrophy in different animals, have to be introduced into this statement, but the fact may be expressed in general terms as above, and the conclusion applied to the human brain. It appears, therefore, that the large cells of the external geniculate body and of the pulvinar belong exclusively to thalamo-cortical neurons; other distributing cells must provide for the varied sight-reflexes which may occur after removal of the occipital cortex.

(*d*) As the result of dissections, Gratiolet, in 1854, came to the conclu-

[1] Von Monakow, Archiv für Psychiatrie, xx. p. 723.

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sion that he could trace, in the monkey, the direct continuation of a portion of the optic tract into the back of the corona radiata. Von Gudden in his earlier researches (1875) traced a degeneration, consecutive upon removal of the occipito-parietal lobe, downward into the optic tract. The existence of this direct occipital tract is generally regarded as proved; it is figured in the schemes of Obersteiner[1] and Testut;[2] but we confess that the evidence upon which it is accepted is somewhat unsatisfactory. The method of dissection when applied to the brain is absolutely untrustworthy, and, although degeneration of the tract may follow a lesion in the occipital cortex, it is so difficult to explain the presence in the cortex of the nutritive centres of the fibres of the optic nerves—*i.e.*, their cells of origin—that we look for some other explanation, and imagine that the descending degeneration is due to vascular or trophic disturbance.

The evidence before us seems to show that most of the fibres of the optic tract which are distributed to the fore-brain end by branching within the external geniculate body and the pulvinar, or reach other parts of the thalamus, particularly its superficial strata, by the stratum zonale. A direct connection with the cortex cerebri is possible, but the observation of a degeneration descending into the optic tract does not seem to throw light upon the question, and we are not aware that any one has, as yet, traced a degeneration ascending directly from the optic nerve into the corona radiata, although the degeneration of the posterior fibres of the corona radiata after enucleation of the eyeball was observed by Panizza[3] so long ago as 1856 as a part of, and presumably consequent upon, the extensive degeneration of the external geniculate body, pulvinar, and anterior quadrigeminal body which follows this operation. Even the degeneration of the corona radiata or the arrest of its growth after enucleation of the eyeball has not, however, been seen by all the observers who have performed this experiment. It was not observed by Von Gudden, Fürster, Ganser, or Von Monakow.

(B) *The Connection of the Optic Tract with the Mid-Brain.*—The corpora bigemina of lower vertebrates are the chief end-stations of the optic nerves. In mammals a second pair of swellings make their appearance behind the bigeminal bodies, and the four swellings together are known as corpora quadrigemina.

As the hemispheres of the great brain increase in size the number of optic fibres going to them increases *pari passu*. Nevertheless in all mammals, man included, a large number, probably the majority, of the fibres still pass to the mid-brain.

Fibres from both the mesial and the lateral roots of the tract pass to the anterior tubercles of the corpora quadrigemina. The fibres of the lateral root sweep over the external geniculate body and turn backward along the

[1] Obersteiner and Hill, Anatomy of Central Nervous Organs, p. 280.
[2] Traité d'Anatomie humaine, 2d ed., vol. ii. p. 621.
[3] Panizza, quoted by Tartuferi.

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anterior brachium of the corpus quadrigeminum. In like manner a certain number of the fibres of the mesial root pass over the mesial geniculate body without interruption in its cells and reach the anterior tubercle, while other fibres reach the same destination by passing between the two geniculate bodies. These last are described by J. Stilling as constituting a "middle root," but it is hardly possible to regard either of these several bundles as separate tracts. In any animal in which, as in the ox (Fig. 6, Plate), the fibre-tracts are large, relatively to the brain, the optic tract spreads into a flat ribbon, the anterior portion of which reaches the external geniculate body and pulvinar, while the posterior portion goes to the anterior quadrigeminal tubercle.

Still a third set of fibres has been described by Stilling,[1] but their existence is so doubtful that we have not thought it worth while to place them in a separate class. It is supposed that a portion of the fibres which pass from the optic tract into the crus cerebri (of which the majority join the sagittal medullary strata as the direct occipital root) turn downward in the crus as a radix descendens, which may be traced, it is said, as far as the decussation of the pyramids. Darkschewitsch[2] says, however, that the fibres of this tract which Stilling regarded as a descending root of the optic nerve acquire their myelin-sheaths before the optic fibres, of which, therefore, they cannot form a part.

Anterior Tubercles of the Corpora Quadrigemina.—Tartuferi[3] described these bodies as presenting a series of strata of gray and white matter,—viz., (1) a superficial layer of very fine white fibres derived from the optic tract; (2) a thin sheet of gray matter containing a small proportion of minute cells; (3) a mass of mixed gray and white matter containing small cells and numerous fine fibres which run sagittally; (4) a second layer of mixed gray and white matter the deeper fibres of which arch over the aquæductus Sylvii. Ganser,[4] who investigated the structure of these bodies with a view to determining the seat of the arrest of development in the mole, still further divides the third layer into three,—viz., (*a*) its superficial layer, which contains numerous fibres; (*b*) its middle layer, or gray nucleus; and (*c*) its deeper layer, consisting of fibres chiefly.

We cannot think that the attempt to divide the extremely obscure tissue of the mammalian corpora quadrigemina into distinct strata is justifiable, except in so far as the stratification is dependent upon the general direction of the fibres which enter these bodies. The fibres of the optic tract spread inward and obliquely backward over their surface. The fibres which leave their gray nuclei on the deep aspect tend to take a ventral course, but are

[1] Bau der optischen Centralorgane, Kassel, 1882.

[2] Die sogenannten primären Opticuscentren, Archiv für Anat. und Physiol., Anat. Abth., 1886. See also other papers by the same author.

[3] Anatomia minuta dell' eminenze trigemine ant., Archivio Italiano per le mal. nerv., 1885.

[4] Gehirn des Maulwurfes, Morphol. Jahrbuch, vii.

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distinguished with difficulty from the arching fibres of the fillet. The fibres which connect them with the cortex cerebri appear to enter them chiefly on their mesial side between the optic fibres and the deep fibres, which may be supposed to connect them with the eye-muscle nerves; the cerebral fibres take a more directly antero-posterior course than either of the other sets.

The gray matter of the corpora quadrigemina consists of a somewhat open ground-substance in which are scattered very minute (15–25 μ) nerve-cells, of pyramidal or triangular shape, with here and there a cell of large size. It is distinctly separated from the gray matter which surrounds the aqueduct by the complex of fibres which curve upward from the tegmental region, and in great part, at any rate, decussate in the dorsal region of the mid-brain. In this book it would be out of place to describe this mass of fibres, which is chiefly connected with the fillet behind and with the posterior commissure in front, and contains, besides, fibres proper to the mid-brain. The arching of the fibres in this region appears to be necessary for their return to the dorsal situation which they occupied in the cord, and from which they were displaced when the spinal canal opened out into the fourth ventricle of the medulla oblongata. We have every reason for thinking that the central gray matter and its investing columns of nerve-fibres are homologous with the gray matter and white columns of the cord, while the gray masses of the corpora quadrigemina are of the nature of a cortex-formation.

In lower animals the elements of which the corpora bigemina or optic lobes are formed resemble those found in the cortex cerebri and present a somewhat similar stratification. The surface is covered by a thick coat of optic fibres, to which succeeds a layer of dense gray matter containing very small cells; then follow regular strata of granules, beneath which again are seen pyramids increasing in size the farther they lie from the surface, and supported on the medullary layer.

The most noticeable feature of the anterior tubercles of the corpora quadrigemina in man and other mammals is the immense richness of the deeper portion of their gray matter in nerve-fibres, which cross one another in all directions and are easily distinguished from the fibres of the medullary substance by their great tenuity. We are inclined to think that the anatomist will most accurately picture to himself the structure of these bodies if he forgets the descriptions which have been given of their stratification, and remembers only that they are covered on the surface by nerve-fibres, and that the gray matter nearest to the surface is almost free from tangential fibres, while such fibres are extraordinarily abundant in its deeper portions.

The Nuclei of the Eye-Muscle Nerves.—The posterior of the nerves which supply the muscles of the eyeball, the sixth, or nervus abducens, pierces the cerebro-spinal axis in the groove between the pons Varolii and the anterior pyramid of the medulla oblongata. It reaches this spot as separate, slightly curving bundles of fibres, which take, except for this curvature, a

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direct course from the globular nucleus, which they leave on its dorsal and mesial aspects. The nucleus lies beneath the floor of the anterior portion of the fourth ventricle, and is visible from the surface, in the brain of a young child, as a rounded swelling in the course of the funiculus teres. Its cells are large and angular.

The fourth or trochlear nerve is the only nerve which joins the axis of the brain on its dorsal side. Its slender cord curves round the crus cerebri in the gap between the cerebrum and the cerebellum to reach the valve of Vieussens, which stretches from the posterior tubercles of the corpora quadrigemina over the front of the fourth ventricle. On the valve of Vieussens this nerve decussates with its fellow of the opposite side.

The third or oculo-motor nerve takes its exit from the brain by large bundles of coarse fibres which pierce the crus along the inner edge of the curious plate of deeply pigmented cells, the substantia nigra, which divides the crus into tegment and crusta. Most of the fibres come from the gray matter on the same side of the brain, but some cross to the opposite side before taking exit.

The whole of the gray matter which surrounds the aqueduct of Sylvius and bounds the back of the third ventricle is given up to the nuclei of the third and fourth nerves, with the exception of a small column of singularly characteristic, round, full-bodied, almost processless cells (diameter 60–80 μ), usually credited to the ascending (or descending[1]?) root of the fifth nerve.

This latter column lies on the same level as the aqueduct and a little to its dorsal side. It is a very striking object in sections through the posterior tubercles of the corpora quadrigemina, not only owing to its crescentic shape and to the remarkable form of the cells, which Deiters[2] described as unlike that of any other cells found in the cerebro-spinal axis, but also on account of their grouping. Towards the front of the column they are placed so close together as almost to touch one another. Deiters compared them to cells of a root-ganglion, such as the Gasserian, but Golgi,[3] who says that they are "absolutely unipolar," believes them to be cells of origin of the fourth nerve. To us this nucleus appears to be allied with Clarke's column and the medullary vagus-nucleus. If its cells give origin to ordinary motor fibres of the fifth or fourth, they differ in a singular way from those of other motor nuclei.

The nuclei of the fourth and third nerves occupy the ventral portion

[1] The cells are described by Ferrier (Brain, vol. xvii. p. 21) as undergoing simple atrophy after section of the motor root of the fifth nerve, to which he thinks that they exclusively belong. This observation, however, raises the whole question of the relation of nerves to the cells in which they take origin. Further information with regard to the time of onset and nature of the changes which occur in a cell after severance from its axis-cylinder process is sorely needed, and we do not feel disposed, until statistical evidence is forthcoming, to attach much importance to appearances suggestive of the "atrophy of disuse."

[2] Untersuchungen über Gehirn und Rückenmark, Brunswick, 1865, pp 91, 92.

[3] Archives Italiennes de Biologie, xix., iii. p. 454, August, 1893.

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of the gray matter, the fourth being posterior and less well defined than the third; for, while the cells of the nuclei of the third are collected into compact groups, those which are generally regarded as giving origin to the fibres of the fourth are more loosely scattered throughout the central gray matter.

The nucleus of the fourth nerve lies beneath the front of the posterior quadrigeminal body. Its cells are large and angular, like those of the nucleus of the third, which will shortly be described, and the fibres which arise from them have, owing to the situation of the nucleus so far in front of their place of exit, a somewhat long course within the brain, curving at first outward, then backward in close connection with the root of the fifth nerve, and finally dorsalward and inward to the valve of Vieussens. A round group of very minute cells which immediately succeeds the nucleus of large cells is by Westphal supposed to be a posterior nucleus of the trochlear nerve.

The several groups of cells which together constitute the nucleus of the third nerve have been mapped out with great precision. They occupy a very considerable portion of the central gray matter, and are also placed outside this gray matter among the fibres of the tegmental region, appearing as the most conspicuous objects in any section through the mid-brain from the level of the groove between the posterior and anterior quadrigeminal bodies for a distance of from seven to ten millimetres farther forward,—a distance which carries us into the back of the third ventricle. The largest of the cells are as large as any of their homologues in the anterior horn of the spinal cord (about 100 μ), and, owing to the quantity of fibres which break up the ground-substance surrounding them, they arrest attention even more forcibly.

The clumps of nerve-cells may be divided into a chief, or posterior, and a smaller, anterior group; or, more naturally, as we think, into (1) the large-celled clumps (cells of about 100 μ in diameter), which probably supply the extrinsic muscles of the eyeball and lie in the ventral and lateral part of the tegment, and (2) the clumps of smaller cells (about 50–60 μ), which give rise to fibres for the intrinsic muscles of the eyeball and lie on the dorsal and mesial side of the large cells, extending also farther forward, towards the third ventricle.

1. The *large cells* are grouped in the following nuclei, from behind forward, on either side:

(*a*) The posterior ventral nucleus.

(*b*) The anterior ventral nucleus.

These two nuclei lie one behind the other in the same sagittal line, resting on the dorsal surface of the mesial portion of the posterior longitudinal fasciculus.

(*c*) The posterior dorsal nucleus.

(*d*) The anterior dorsal nucleus.

The isolation of these four nuclei is hardly sufficiently distinct to justify

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their description as separate; they might be considered as forming together the "lateral nucleus." (Obersteiner.)

(*e*) In the middle line lies an unpaired almond-shaped "central" nucleus.

2. *Small cells.* (*a*) A large roundish nucleus of smaller cells lies to the dorsal side of the large-celled clumps and nearer the middle line than any of the latter, save the central nucleus. It is the posterior of the small-celled nuclei, or nucleus of Edinger and Westphal.

(*b*) The mesial anterior small-celled nucleus is found at the level of the posterior commissure and lies close against the raphé, by which alone it is separated from its fellow of the opposite side.

(*c*) The lateral anterior small-celled nucleus lies on a level with the aqueduct of Sylvius in the back of the third ventricle.

The exact correspondence of these nuclei with the physiological centres for the muscles of the eye as mapped out by Hensen and Völckers has not been proved, but the anatomical position of the nuclei coincides so nearly with the situation of these centres as determined by experiment that we feel justified in attaching some importance to the coincidence, and in concluding that we know within a very little the muscles to which their fibres are distributed.

In searching out any object in the field of vision and bringing the eyes to a focus, it appears that an animal calls into action the several members of a series of centres which occupy the hind- and mid-brain, beginning first with those which are situate farthest back. By the centres for the muscles of the head and neck the head is placed in the right position. Next the external recti muscles are set in action by impulses which proceed from their centres in the front of the floor of the fourth ventricle, and the eyes, which were probably at the time converged upon the sward on which the animal was feeding, are immediately rendered parallel to each other. Then the several extrinsic muscles raise the lids and the eyeballs and direct the gaze rapidly over the field until the suspected object is in view. The internal recti then cause them to converge to the appropriate degree. Only now, when the extrinsic muscles have done their work, do the nuclei of the nerves to the intrinsic muscles play their part, and of these the centre for the pupil is the first to act. Finally, and only after all these mechanisms are adjusted,—the eyes brought to bear upon the object and converged at the right angle for the distance, and the pupil properly regulated so that it admits no more light than may act upon the retina without risk of injuring its tissue,—is the light focussed upon this sensitive screen.

Adamük succeeded in evoking movements of the eyeballs by electric stimulation of the cortex of the corpora quadrigemina. Hensen and Völckers, applying their electrodes to different spots in the gray matter which surrounds the aqueduct of Sylvius and spreads out at the back of the third ventricle, called forth movements in the sequence which we have just described as the natural sequence of events preceding the direct vision

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of an object to which our attention has been called by indirect vision or by hearing. Such pathological observations as have been made as yet confirm this location of centres, although not unequivocally. Kahler and Pick observed that when the levator palpebræ, rectus superior, and obliquus inferior muscles, which act together in raising the eyes, are paralyzed, the posterior and lateral bundles of the oculo-motor nerve are found to have undergone degeneration. Starr,[1] by analyzing twenty cases of partial oculo-motor paralysis, was able to make a map of the centres for the several muscles which is not improbably correct. Many more cases, however, accurately observed, are needed before the several groups of cells can be allocated to the muscles which they innervate respectively, with any certainty whether the reflection of optic impulses, the actual junctions between afferent and efferent fibres, the transference by "physiological contact" of impulses from the retina into motor channels, occur in the immediate vicinity of these cells or at some higher level.

The sum of such physiological and pathological evidence as we possess at present points to the conclusion that the mesial small-celled nucleus (2, *b*) supplies the ciliary muscle, and the lateral small-celled nucleus (2, *c*) the sphincter iridis; while we know nothing as to the functions of the nucleus of Edinger and Westphal. It is possible that the nucleus last named has nothing to do with ocular movements. The fibres for the rectus internus probably originate in the cells of the anterior ventral large-celled nucleus (1, *b*), but this is much disputed. For the purposes of conjugate deviation a connection seems to be required between the nucleus for the external rectus of one side and the nucleus for the internal rectus of the other. Such a connection has been described, but a study of the literature of the subject seems to suggest that neurologists have been occupied in designing a mechanism capable of doing the work which we know to be required of the mid-brain, rather than in unravelling the structure of this region as it is found to exist.

The Connection of Optic Fibres with the Nuclei of the Eye-Muscle Nerves.—The mid-brain contains the mechanism for the reflection to muscles appropriate for the execution of instinctive movements of impulses which travel up the optic nerve, and especially to the muscles of the eyeballs. In lower animals these reflex actions are probably carried out solely by the mid-brain, while in mammals much of the work hitherto done by the mid-brain is transferred to, or strictly supervised by, the great brain. There does not appear to be much risk in generalizing as to the plan of disposition of the elements of the apparatus in animals with large optic lobes; in fishes and birds the fibres of the optic nerves are distributed over the surface of the mid-brain; they sink down into the substance of the optic lobes, in which each breaks up into a brush of fibrils which bear "granules." The larger cells of the deep strata of the optic lobes belong to neurons the axis-cylinders

[1] Journal of Nervous and Mental Diseases, May, 1888.

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of which end in the gray matter surrounding the cells of the eye-muscle nuclei. These cells, again, belong to neurons of which the axis-cylinders constitute peripheral nerves. Afferent optic fibres and efferent motor nerves are therefore connected through the intervention of a single set of neurons of the optic lobes. While it is most probable that a similar arrangement obtains in the higher mammals, the anatomist looks with astonishment at the poverty in cells of their corpora quadrigemina. Optic fibres spread over their surface, and from beneath them fibres seem to make for the nuclei of the third and fourth nerves; but the gray matter which intervenes between the two sets of fibres and also gives origin to the fibres which connect the corpora quadrigemina with the great brain appears insufficient to provide the connecting neurons.

If what has been said as to the connections in the brain of the optic and motor-oculi nerves be summed up, it will be recognized that the *fundamental plan of the nervous mechanism* has yet to be worked out.

According to the older and simpler view the optic nerve only contains afferent fibres. These are of two kinds,—for the conveyance of visual impulses, and impulses determining movement of the eyeball respectively. Impulses of sight, properly so called, are carried to the cortex cerebri *via* the optic thalamus; impulses of sight-adjustment are carried to the mid-brain for reflection to motor nerves. The cortex cerebri and mid-brain are united by ascending and descending fibres. It is no longer possible to believe in so simple a scheme, for it is necessary to admit that the cortex cerebri, as well as the thalamus and mid-brain, is the seat of visual reflexes. Such a semi-diagrammatic separation of afferent tracts is, therefore, unjustifiable. Further, it is urged on various grounds that efferent fibres are distributed to the retina. These are supposed to come from the mid-brain, and to be recognizable in the optic nerve, owing to their small size. Conclusions have somewhat outstripped evidence in this matter. It is desirable that judgment should be suspended until it has been proved that the small fibres are alone connected with the mid-brain; and, further, until an intelligible explanation has been given of the efferent functions of these small fibres which so vastly preponderate in the optic nerve.

THE VISUAL AREA OF THE CEREBRAL CORTEX.

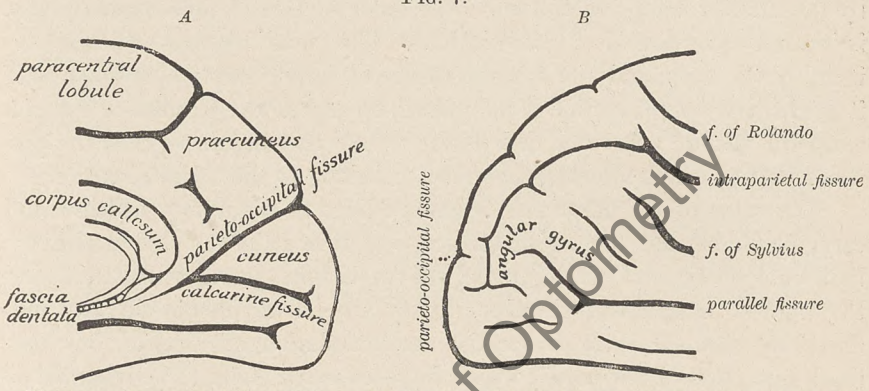
The cortical territory of optic fibres lies at the back of the hemisphere. That optic fibres are distributed to the occipital lobe, including its mesial surface (the cuneus),—the term lobe being used in a general sense and not limited to the area so defined in descriptive anatomy,—has been proved beyond the possibility of doubt. This is the sphere of the brain of which the action is determined and controlled by visual impulses. Its exact delimitation has, however, hardly been accomplished as yet.

Anatomical Evidence.—There is nothing in the arrangement of the convolutions, or of the fissures by which they are bounded, which clearly marks out the frontiers of the visual sphere. The writer some ten years

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ago studied all the brains of different animals preserved in the museums which were then accessible to him, and particularly the rich collection in the museum of the Royal College of Surgeons of England made by the late Sir Richard Owen, in the hope that he might be able to devise some plan of mapping out the cortex by means of its fissures into areas related to the several nerves or groups of nerves of sense. He hoped to be able to establish a relation in size between the cross-section of, or number of fibres in, each of the cranial sensory nerves and the area of the cortex to which its impulses are distributed. Although the attempt to obtain exact numerical data was a complete failure, owing to the number of "variables" involved in the calculation, the result, if expressed in general terms, is sufficiently striking. It is easy to show by photographs and tracings that animals in which the sense of smell is acute have large temporal lobes; acute hearing is accompanied by fulness of the brain about the end of the fissure of Sylvius; a large fifth nerve goes with great development of the region which lies below and behind the motor area; while the occipital region is strongly developed in animals which depend mainly on the sense of sight.

FIG. 7.



Diagrammatic representations of the occipital region of the right cerebral hemispheres: *A*, from inner; *B*, from outer aspect. (One-third natural size.)

Since these observations were published, the division of the brain into territories occupied by the secondary connections of the sensory nerves has been placed beyond doubt. The nerve of sight carries its commerce to the occipital region, or, at any rate, its chief relations are with this area, for it is not impossible that it may be connected also in a less concentrated degree with other parts of the cortex.

Topography of the Occipital Region.—We purposely avoid the word lobe, since there is no reason to attach any morphological significance to the lines adopted as the landmarks between the occipital and parietal or occipital and temporal lobes of human anatomy. The occipital region of the great brain is prolonged backward over the cerebellum as a three-sided pyramid. The fissures on its outer surface (Fig. 7, *B*) are irregular and inconstant. Those on its under surface are more constant, but they are

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common to the occipital and temporal lobes, and the extent to which they are prolonged backward is subject to considerable variation. Only on its mesial aspect (Fig. 7, *A*) are the fissures deep and regular, but on this side they are so remarkable as to suggest the idea that they are landmarks of great importance. The deep parieto-occipital fissure, which appears also on the outer surface of the brain, is prolonged forward until it almost reaches the portal margin of the cortex,—*i.e.*, until it nearly cuts the gyrus fornicatus in two. It is joined by the calcarine fissure, a "total" fissure which causes a swelling (the hippocampus minor) in the third ventricle. A well-defined lobule, the cuneus, is thus marked off by the parieto-occipital fissure above and in front and the calcarine fissure below. The collateral or inferior occipito-temporal fissure, which is also a total fissure (giving rise to the eminentia collateralis in the descending horn of the ventricle), cuts deeply into the occipital and temporal lobes. Between the calcarine and collateral fissures lies the gyrus lingualis, or gyrus occipito-temporalis medialis. Below the collateral fissure, and forming the transition between the inner and under aspects of the occipital region, comes the fusiform or inferior occipito-temporal convolution, which in turn is bounded on the outer side by the inferior temporal fissure. The outer surface of the occipital region is in some cases devoid of convolutions. The small fissures which groove it are never deep, and the nearest fissure of importance which looks as if it might be a boundary line is the turned-up end of the parallel or superior temporal fissure. Around this fissure hooks the angular gyrus, the posterior half of which appears, therefore, to belong to the occipital region.

The value of the fissures as boundary lines is a question which would carry us far beyond the legitimate scope of this article. Their constancy, both ontogenetic and phylogenetic, proves beyond question that they have the highest morphological value. They are not accidental furrows produced by skull-pressure or for the accommodation of arteries, but they mark out parts of the cortex which have as much claim to be regarded as separate organs as have the fingers or the toes. When, however, we endeavor to settle their territorial significance we find our judgment divided between evidence of different, apparently of antagonistic, bearing. Certain fissures (*e.g.*, the parieto-occipital and the fissure of Sylvius) seem to separate organs of different function, while others (*e.g.*, the fissure of Rolando and [?] the calcarine fissure) appear to lie in the centre of the lobe to which they belong, to represent, as it were, its most concentrated function. It is possible that we include under the common term two kinds of groove of entirely different origin and meaning, one kind of fissure being the valley which separates two bulging lobes, the other the depression which appears in the centre of a lobe when sufficient surface for its cortex cannot be provided otherwise. Beyond pointing out the apparent importance as landmarks of the parieto-occipital and parallel fissures, anatomy can do little to settle the vexed question of the boundary of the optic region of the cortex.

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Pathological Evidence.—The observation of the degenerations which result from disease or artificial destruction of the eyeballs, and conversely the determination of the situation in the brain of all the lesions which have given rise to blindness, have probably contributed in a larger degree than any other kind of research to the localization of the visual area. Atrophy consequent upon disease or destruction of the eye would supply the more important class of evidence if the changes in the brain were sufficiently distinct for recognition. As stated already, however, certain observers have been unable to detect any alteration in the great brain after enucleation of the eyeball, even when the operation was performed on new-born animals. Atrophy of the occipital lobes consequent upon early disease of the eye has been described, but the boundaries of the atrophied area cannot be marked out.

A very large number of cases of cortical hemiopia or amblyopia have been observed. Such cases have been described or collected by Luciani and Tamburini,[1] Nothnagel,[2] Angelucci,[3] Bellouard,[4] Mauthner,[5] Exner,[6] Wilbrand,[7] Haab,[8] Starr,[9] Seppilli,[10] Philipsen,[11] Seguin,[12] Bouveret,[13] Chauffard,[14] Déjerine,[15] Von Monakow,[16] Henschen,[17] and others. Henschen collects and analyzes one hundred and seventy-one cases. In a recent memoir Vialet[18] also has given a very careful analysis of a large number of selected cases, adding others which he had himself observed.

This anatomico-pathological research offers very peculiar difficulties, and still further statistics are necessary before the evidence from cortical lesions can be said to be decisive. In comparatively few of the cases was the cortical lesion clearly circumscribed, and even when this condition is fulfilled it has still to be asked, What other functional disturbance was produced as well as blindness? How far did the lesion extend beyond the visual area? And, again, Was the blindness due to the focal lesion, or did

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[1] Studi clinici sui centri sensori corticali, Milan, 1879; also Luciani, in Brain, 1884.
[2] Topische Diagnostik des Gehirnkrankheiten, Berlin, 1879.
[3] Raccoglitore med., Forli, 1880, etc., transl. in Rec. d'Ophthalm., Paris, 1889.
[4] De l'Hémianopsie, Paris, 1880.
[5] Gehirn und Auge, Wiesbaden, 1881.
[6] Untersuchungen über die Localisation, 1881.
[7] Hemianopsie, Berlin, 1881.
[8] Klinische Monatsblätter.
[9] American Journal of the Medical Sciences, 1884.
[10] Luciani and Seppilli, 1885, German trans. by Fraenkel (Functions Localisation), Leipsic, 1886.
[11] Bibliothek for Laege, 1885.
[12] Journal of Nervous and Mental Diseases, 1886, and Archives de Neurologie, 1886.
[13] Lyon Médical, 1887.
[14] Revue de Médecine, 1888.
[15] Archives de Physiol., Paris, 1890, p. 177.
[16] Loc. cit.
[17] Pathologie des Gehirns, Upsala, 1892.
[18] Les Centres cérébraux de la Vision, Paris, 1893.

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the disease give rise to pressure or secondary degenerations and thus cause blindness by an indirect action?

Henschen[1] concludes that the visual area is limited to that portion of the cortex which is sunk within the calcarine fissure. Within this fissure and for a short distance on the adjacent convolutions the cortex is distinguished by the presence of Vicq d'Azyr's (or Gennari's) band, a sharply defined white band due to the presence of a sheet of tangential fibres. Henschen's conclusion is chiefly based on a case described by himself and Nordenson in which the lesion was limited to this area, together with cases of disease of the eye and blindness in which histological study showed atrophy of nerve-cells in this area. He is further of opinion that it is possible to ascertain the projection of the retina on the cortex; the dorsal quadrant of the retina being represented in the upper lip of the fissure, the ventral quadrant in the lower lip, the macula lutea in the front of its floor, and the peripheral end of the horizontal meridian at its back. Since loss of one eye entails histological changes in the cortex on both sides of the brain, he concludes that each cortical visual area belongs to corresponding parts of both eyes.

Von Monakow concluded, from the cases which he first observed, that the visual area is localized on the inner surface only of the occipital lobe, "the domain of the calcarine fissure." A subsequent observation has induced him to extend the area so that it includes the external surface of the occipital lobe and even the angular gyrus.

Certain other pathologists have concluded, on the strength of cases which have come under their notice, that the lingual and fusiform convolutions also form part of the visual sphere.

Experimental Evidence.—Since of necessity this evidence relates to the localization of the visual area in animals and not in man, we have placed it last. Had it been applicable without qualification to the problem before us, we should have regarded it as more satisfactory than clinical evidence, inasmuch as it can be more exactly controlled.

Experiments upon the brain take two forms, which are complementary one to the other. In the first place, removal of portions of the cortex abrogates certain of the animal's sensory endowments. In the second place, electrical stimulation of spots on the cortex which lie outside the "motor area" induces movements which have the appearance of being adaptive movements such as commonly result from the provocation of sense-presentations.

The results of each kind of experiment must be interpreted with full knowledge of the risk of the introduction of error from causes which are only just beginning to be understood. The necessary reservations may be briefly summed up as follows:

(1) Localization of function in the cortex may be described as rapidly

[1] Henschen, loc. cit., p. 358.

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progressive. It cannot be defined in the rabbit's brain; in the dog it is ill defined; in the monkey it is fast becoming precise. In man alone is it permanent. In the lower animals the sensori-motor functions are settlers in the cortex. In man they have acquired the freehold, the value of their title increasing as they become specialized. It is the skilled trades only which have an absolute right to the areas they occupy. The very existence of so highly skilled a function as that of speech depends upon the integrity of the mechanism by which it is carried out, and which has been built up by a laborious process of training. The passage of impulses determines the growth of tissue. The development of tissue facilitates the passage of impulses. This function of speech is taken as an illustration of the most elaborate and human of the motor functions of the brain,—a function which, on account of its intricacy, has fixed its seat immovably in the cortex, taking complete possession of a spot convenient for its commerce; even limiting its residence to one side of the brain, despite the symmetrical situation of the muscles of the mouth and larynx by which it is expressed. The consideration of this extreme case puts us on our guard in applying the results of experiments upon animals to the elucidation of the functions of the human brain.

(2) The lower the animal in the scale of existence the more elaborate are the reflex actions carried out by the subcerebral mechanisms. The cerebrum of a rabbit, still better that of a pigeon or a frog, may be removed completely, and yet the animal will respond to stimulation of its retina in a manner which often seems purposeful. It is quite possible that the dogs from which Goltz removed the whole occipital cortex may have been deprived of conscious vision,—"conscious" is perhaps too definite a term, while "psychical vision" is incapable of definition,—although the impulses which travelled up the optic nerve clearly found their way, through the parts of the brain which were left, to the motor nerves of the muscles by which the animal executed appropriate movements.

(3) The central nervous system does not consist of isolated organs, but is a sympathetic and subtly interdependent whole. The force of the knee-jerk is modified, as Lombard and Bowditch have shown, by impulses passing through parts of the cerebro-spinal axis far distant from its reflex centre. It is easy, therefore, to understand that any operative interference with the brain produces an action, presumably irritative in nature, by which cerebral mechanisms, not immediately affected by the operation, are thrown out of gear. Until it has been ascertained that the phenomena observed after the operation were not the effects of shock, they must not be held as indicating that the part removed was responsible for the functions which seem to be lost. It is generally supposed that the effects of shock wear off, and that after an interval, very differently estimated by different observers, the loss of function proves the destruction of the apparatus by which it was performed.

(4) Inflammatory swelling, secondary degenerations, etc., may affect parts of the brain supposed to have been left intact.

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(5) The production of movements by electric stimulation of the occipital cortex has not as yet been brought into line with the production of movements by stimulating the motor area. A stronger stimulus is required. The movements follow after a longer latent period and are irregular and uncertain. They are easily antagonized by stimulation of the motor area. Their character is not much affected by slicing away the cortex. In short, they are hardly sufficiently definite to be taken as proving the existence of sight-movement reflexes, although they confirm the conclusion which is based upon other evidence that the occipital cortex contains the visual area.

After this introduction a brief summary of the results of experiments upon animals will suffice. Observations upon dogs indicate that the cortex of the occipital region is concerned with vision; they throw no light, however, upon the problem before us,—viz., the exact topography of the visual area in man. Upon evidence which is now generally regarded as insufficient, Munk[1] concluded that he could map out the visual sphere in such a way as to represent the projection of the retina upon the brain. If subsequent observers find in the dog or other animal any similar association of the several portions of the retina with the several parts of the visual sphere, it will lead us to look for a similar allocation in man.

Numerous ablation-experiments have been performed upon the brain-cortex of monkeys. All observers agree in asserting that enduring visual disturbance is produced only when the back of the brain is operated upon, but the delimitation of the visual sphere and the exact effect of its removal upon vision are variously described.

Extent of the Visual Area.—Munk,[2] Horsley,[3] Schäfer,[4] and Sanger Brown regard it as limited to the occipital lobe. Luciani[5] considers that the parietal and temporal lobes are also connected with vision, although the most exclusively visual centre is situate in the occipital lobe.

Ferrier[6] looks upon the angular gyrus as more important than the occipital lobe, inasmuch as it contains, he thinks, the special region of clear or central vision of the opposite eye, and perhaps to some extent also of the eye on the same side, while only the correlated halves of the peripheral portions of the retinæ are represented in the rest of the occipito-angular region.

Effect upon the Field of Vision of Removal of the Visual Area of the Cortex.—All observers agree that unilateral decortication produces hemiopia towards the opposite side of the field of vision. There is great difference of opinion as to the amount of amblyopia which accompanies the hemiopia,

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[1] Zur Physiologie der Grosshirnrinde, 1881.

[2] Op. cit.

[3] Horsley and Schäfer, Philosophical Transactions of the Royal Society, 1888, vol. clxxix., B, p. 1.

[4] Schäfer and Sanger Brown, ibid., 1888, vol. clxxix., B, p. 303.

[5] Brain, 1884.

[6] The Functions of the Brain, 2d ed., p. 288.

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and as to whether it is only the opposite eye which is rendered everywhere less sensitive or whether vision is also obscured on the otherwise unaffected half of the retina of the same side. The extreme difficulty of testing vision in animals renders a discussion of the various opinions on this subject undesirable.

The Curtailment of the Animal's Endowments.—There are three possible views as to the effect of the operation upon the animal's faculties, and each view has its advocates.

(1) The removal of the cortex may abolish visual sensations of every description. The impulses projected up the optic nerve from the stimulated retina may come to an end in the injured tissue,—be lost in the lesion,—producing no effect upon consciousness and no transformation of energy within or without the body.

This is certainly not the case in lower animals. The further we descend the animal scale the more open do we find the subcortical reflex-paths to be. In the lower animals sensory impulses find their way into motor paths without the intervention of the great brain. Longet showed that rabbits and rats deprived of the cerebral hemispheres (the optic thalami being left intact) execute certain movements in response to light. Vulpian[1] repeated these experiments, and suggested that we should speak of these mutilated animals as retaining "sensations" of sight although their "perceptions" are abolished. There is reason to think that in the monkey (and still more in man) even such primitive reflex actions are so far subject to the control of the great brain that they cease to be possible after its removal. Schäfer and Sanger Brown tested with all the thoroughness possible a monkey from which the occipital lobes had been removed nine months previously, for the purpose of determining whether the animal had any power whatever of discriminating between light and darkness. Although in this instance they were seeking for evidence of a survival of sight-perceptions, the tests they used would in the rat or rabbit have caused some reflex response. This monkey, however, bore light flashed into its eyes without making the slightest movement, although its pupils reacted normally. Ferrier describes experiments of a similar kind, and we seem to be justified in concluding that, with the exception of the pupil-reflex, the occipital cortex is in the Primates the only seat of the reflection of visual impulses into motor channels; for there can be but little doubt that the small size of the quadrigeminal tubercles and the retrograded structure of their cortical tissue indicate that their office is less important in higher than it is in lower animals. The large optic lobes of reptiles and birds are covered with gray matter formed upon what may be regarded as essentially the cortex type, and therefore fitted, we are justified in supposing, for the discharge of duties which in the Primates have been assumed by the cerebral hemispheres.

If this be true, removal of the cortex in the monkey abolishes not only

[1] Physiologie du Système nerveux, p. 709.

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perception but also sensation. It is probable, however, that when a part of one side of the brain is removed the sensory impulses which are accustomed to produce their effects on this part may be received by the opposite side, or they may even find attention from other and intact parts of the same hemisphere, or, at any rate, from the remaining part of their own sensory zone.

(2) It may be that removal of the visual area abolishes consciousness for sensations of sight. The blindness is absolute if this be the case, since impulses, so long as this condition lasts, do not give rise to perceptions, although they may provoke reflex actions. Many physiologists prefer to avoid the psychological question, but Ferrier, among others, takes this view.

(3) Munk introduced the conception that, since the cortex is the storehouse of visual memories, the blindness which follows its removal is due not to the abolition of current perceptions, but to the extinction of those which were stored away in the cortex. A new presentation of sense conveys henceforth no meaning to the animal, since it has no experience with which to compare it. It is in Munk's terminology "psychically blind." The proof of this theory will depend upon the possibility of re-educating an animal from which the existing visual sphere has been totally removed.

Duration of the Effects of Decortication.—Ferrier holds that when an operation is complete and successful, the whole of the visual areas on both sides of the brain (including the angular gyri) being removed, without inflammatory sequelæ, the blindness is complete and permanent. Schäfer and Sanger Brown obtained a similar result in one case without destruction of the angular gyri. Luciani, on the other hand, asserts that even after the most extensive extirpation of the occipito-temporal area absolute blindness does not persist beyond a few days, when its place is taken by complete "psychical" blindness, which in turn becomes incomplete, although it remains permanently. The animal again makes use of the sense of sight in searching for its food, although it never learns to distinguish by this sense alone between widely dissimilar bodies, such, for example, as meat and sugar.

Summary.—The evidence before us leaves no doubt as to the connection with vision of the posterior part of the cerebral hemisphere, but the conflicting statements of those who have investigated the subject leave us in uncertainty both as to the topography of the visual sphere and also as to the nature of the processes which are carried on within it. The balance of evidence is in favor of complete limitation of vision to this sphere in monkeys and man, rather than the concentration in this region of a function shared in a lower degree by other parts of the cortex. There is, too, positive evidence that when the whole area has been removed vision is lost, other parts of the cortex being unable to acquire the faculty; whereas if but a small part of the visual sphere be left intact the animal gradually learns to work so well with the part that is left that its vision becomes almost as good as before.

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Speculations as to the nature of the activities of the cortex-centres appear to us to be barren in the present state of physiological psychology. "Sensation," "perception," "sense-judgment," are most valuable terms when used to classify subjective observations. Their use in physiology is allegorical. Until we know something of the nature of the changes effected in the central nervous system by the receipt of afferent impulses, it is useless to speculate as to whether a particular portion of nerve-tissue may contain the memories of sensory impressions and yet not be the tissue in which current sensations become conscious, or whether it may be the tissue in which sensations light up consciousness, but not the tissue in which the motor response to unfelt sensations originates.

It appears to us sufficient to say that in the highest mammals removal of the occipital cortex produces blindness, whereas in lower mammals vision is only partially destroyed by the same operation.

CONNECTIONS OF THE OCCIPITAL CORTEX WITH THE LOWER VISUAL CENTRES.

The white matter of the occipital lobe forms a dense cone, hollowed out by the posterior horn of the lateral ventricle. On the outer side of the ventricle the wall is everywhere very thick; on its inner and under sides the calcarine and collateral fissures cut so deeply into the wall as to leave but a thin shell of white matter between the ventricle and the cortex. Many attempts have been made to disentangle the several tracts of fibres which together make up this dense medullary mass, but without any particularly useful results. The following groups of fibres enter into its constitution.

(1) Short fibres, or fibræ propriæ, which unite together different parts of the same or adjoining convolutions. These intergyral commissures form a sheet immediately beneath the cortex.

(2) Long intra-hemispheral commissures. These lie below the fibræ propriæ, and constitute many tracts of varying length, breadth, and distinctness. None of these tracts is more easily distinguished by dissection than the inferior longitudinal fasciculus, or more easily followed with the naked eye or with the microscope through a series of sections stained after Weigert's method in hæmatoxylin and decolorized with potassic ferridcyanide or potassium permanganate. It runs as a broad band from the anterior end of the temporal lobe to the occipital pole. Sagittal fibres beneath the fibræ propriæ on the outer surface of the lobe constitute a distinct sheet or bundle (fasciculus occipitalis perpendicularis) from the neighborhood of the gyrus angularis to the gyrus fusiformis. Other shorter tracts or sheets of fibres have been described as proper to this region, but, when it is realized that practically every part of the cortex of the great brain is connected by "association fibres" with every other part, it will be doubted whether it is desirable to give a name to each associating tract which is found to be somewhat distinctly segregated from the general mass.

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If ever our knowledge of the functions of the cortex is more detailed, it will be necessary to look out for evidence of unusually intimate union between this convolution and that. At present we may be content to mention, without describing, the stratum calcarinum, which unites the lips of the calcarine fissure, the stratum proprium cunei, for the most part longitudinal, the stratum cunei transversum, and the fasciculus transversus lobuli lingualis. The names given to these several tracts indicate their general disposition.

(3) Interhemispheral fibres of the corpus callosum. The fibres of this vast commissural system are largely responsible for the thickness of the outer wall and floor of the posterior horn. Instead of crossing directly from occipital lobe to occipital lobe, the posterior fibres of the corpus callosum are gathered up into a thick beam (the splenium). From this, after crossing in the roof of the third ventricle, they sweep backward on either side in the forceps posterior, keeping close to the lining epithelium of the posterior horn, for which they form an imperfect sheath, the tapetum. From this sheath fibres stream to every part of the occipital cortex; those which reach its inner wall curve round the posterior horn.

(4) In addition to the "association fibres," connected at both ends with the cortex, the medullary substance of the occipital lobe is made up of "projection fibres," or fibres of the corona radiata. It is customary to name these, in a vague way, the "optic radiations of Gratiolet," although, as we have already shown, Gratiolet's description applies not to the mass of fibres, but to those which he supposed he could trace into the optic tract.

Between the tapetal fibres which sheathe the ventricle and the commissural fibres which line the cortex, the medullary mass is made up of interwoven radiating and tangential fibres. Owing to this intermixture of elements crossing one another at various angles, rather than to any peculiarity in calibre or reaction to staining agents, the central mass appears, especially when treated after Weigert's method, much lighter than the compact bundles of fibres by which it is surrounded. This must not be regarded, however, as a character distinguishing the tracts of which it is composed.

What is the destination of these tracts? Our answer is based upon presumptive evidence rather than observation. (*a*) They unite the cortex cerebri with the cortex cerebelli, especially its upper or anterior surface. (*b*) They certainly unite the cortex with the optic thalamus, both directly and through its stratum zonale, and also with the external geniculate and anterior quadrigeminal bodies. To these fibres the name "optic radiations" would be most appropriately applied. (*c*) They also unite the cortex with the back of the internal capsule and therefore with the sensory gray matter of the cerebro-spinal axis. (*d*) Possibly they contain fibres of the optic tract which are not interrupted in the basal gray matter. The fibres which are added to the back of the internal capsule from the pulvinar and from the anterior quadrigeminal and external geniculate bodies form a mass,

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shaped like a cornucopia, with its broad end directed backward and downward. Its more condensed handle, which curves at first forward and outward, then upward and backward, is sometimes termed the "sagittal tract of Wernicke," or, with even less precision, the "intra-cerebral optic tract."

In addition to these, which are chiefly ascending tracts, the results of physiological experiment lead us to look for (*e*) fibres descending to the nuclei of the eye-muscle nerves and perhaps to other motor nuclei farther down the axis.

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CONGENITAL MALFORMATIONS AND ABNORMALITIES OF THE HUMAN EYE.

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DEVELOPMENT OF THE EYEBALL AND ITS APPENDAGES.

Before describing the various congenital abnormalities to which the eye and its appendages are liable, it is well to give a brief outline of their mode of normal development.

The first stage in the formation of the eye commences exceedingly early in fœtal life. By an outgrowth of the wall of the anterior cerebral vesicles is produced the primary optic vesicle, the connection of which with the brain becomes gradually more and more constricted, forming a stalk, in which afterwards is developed the optic nerve. The cavity of the primary optic vesicle communicates at first with the cavities of the cerebral vesicles through this stalk. The next stage consists in an involution of the primary optic vesicle. By the involution of its anterior surface a cup is produced, the secondary optic vesicle, into which passes a downgrowth from the superficial epiblast; this downgrowth subsequently becomes cut off from the rest of the surface epiblast, and forms the lens vesicle. The lower surface of the primary optic vesicle also becomes involuted by an upgrowing process of mesoblast, which afterwards develops into the vitreous humor. This involution below extends backward for a short distance into the stalk of the primary optic vesicle. The cup of the secondary optic vesicle has two layers, which are continuous with each other at its margin. At first the cup is imperfect below, due to the involution which has taken place there. This gap constitutes what is known as the fœtal ocular fissure. It is at first wide, but gradually becomes narrower, and is at last closed altogether, thus shutting off the mesoblast in the interior of the eye from that external to it. The outer of the two layers of the secondary optic vesicle remains as a single row of cells, which later become pigmented and form the pigmented layer of the retina; the inner becomes thickened, being subsequently differentiated into the other layers of the retina.

The lens vesicle is, as we have said, formed by a downgrowing process of cuticular epiblast, which gradually becomes shut off from the surface epiblast: this shutting off is effected by the intrusion of mesoblast between them. From the anterior portion of this mesoblast is developed the sub-

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stantia propria of the cornea, and from the posterior part the anterior fibro-vascular sheath of the lens.

In the mesoblastic tissue which grows up into the interior of the secondary optic vesicle a blood-vessel forms, the hindermost part of which remains permanently as the central artery of the retina; the anterior part persists for a short time as the central artery of the vitreous. This artery breaks up at the posterior pole of the lens into branches, which are distributed over its posterior surface in what is called the posterior fibro-vascular sheath; prolongations from this are continued forward round the sides of the lens to join the anterior fibro-vascular sheath; in this way the whole lens is encircled by blood-vessels. Meanwhile the lens vesicle has undergone considerable changes. The cells on the posterior wall have lengthened out, and in so doing have filled the whole of the cavity of the vesicle. The cells on the anterior wall have remained unchanged, or become somewhat flattened. The cells in the centre of the posterior layer elongate the most; at the sides there is a gradual transition to the ones which have undergone no change. It is in this transitional zone that fresh lens-fibres are subsequently laid on. The cells of the anterior layer proliferate, multiply, and shift round on the inner surface of the capsule towards the transitional zone, where they lengthen out into fibres; as these lie behind the fibres formed from the original posterior layer of cells, the latter come to constitute the nucleus of the lens. As the tension in the capsule increases, the fibres get more and more flattened out, and their nuclei disappear.

The capsule of the lens very early makes its appearance. There are two views as to its mode of origin: one, that it is a cuticular deposit from the epithelial cells of the lens itself, and the other, that it is derived from the mesoblastic fibro-vascular sheath; the former is the more probable.

The suspensory ligament is formed from adhesions which take place between the fibro-vascular sheath of the lens and the ciliary processes while these structures are in contact,—*i.e.*, about the third month. As the eyeball grows, the ciliary processes become separated from the sides of the lens, and the adhesions, which are at first cellular, become lengthened out into fibres.

The mesoblastic tissue which surrounds the outer layer of the secondary optic vesicle is at first a mass of round cells, and no differentiation can be made out between the sclerotic and choroid coats; later the inner part is vascularized, and the tissue between the two coats becomes spaced out; pigment does not form in the choroid until the seventh month, sometimes later. The ciliary processes develop about the third month by folds forming in the two layers of the anterior portion of the secondary optic vesicle, into which mesoblastic tissue extends and becomes vascular. The iris is produced by an extension inward of mesoblast from the anterior portion of the ciliary body, together with the two layers of the secondary optic vesicles on its posterior surface. The posterior or inner of these two layers is at first, like the corresponding layer on the inner surface of the ciliary body, unpigmented; but later pigment develops in it. The iris grows inward

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beneath the anterior fibro-vascular sheath, and has to insinuate itself between it and the cornea on the one side and the lens on the other; as it does so it pushes the prolongation from the posterior fibro-vascular sheath in front of it. Its stroma is unpigmented until after birth. The central portion of the anterior fibro-vascular sheath left stretching across the pupil forms the pupillary membrane, which disappears before birth. The periphery of the anterior fibro-vascular sheath, beneath which the iris grows, becomes incorporated with that structure and forms its anterior layer. As the eyeball increases in size, the central artery of the vitreous becomes stretched, the circulation of the blood through it becomes arrested, and both it and the posterior fibro-vascular sheath disappear.

The upper and lower eyelids commence early as protrusions of the integument a short distance from the corneal margin; these continue to grow, and ultimately their margins meet and unite in front of the globe. The cavity which is thus enclosed forms the conjunctival sac. The Meibomian glands and the follicles for the cilia commence to form during the adhesion of the lids, by the downgrowth into the mesoblastic connective tissue of the lids of solid columns from the rete Malpighii. A short time before birth the epithelial connection along the margin of the lids gives way, and they again become separate.

The lacrymal gland is developed, about the third month, by the downgrowth of a solid mass of epithelium from the upper and outer portion of the conjunctival sac; branches subsequently jut out from the central mass, and thickenings form on these; then the central cells of each branch undergo a fatty degeneration, and so become tubular.

The lacrymal ducts are developed in the groove which is early formed between the maxillary processes externally and the outer nasal processes internally; whether from an adhesion of the edges of the groove or from an epithelial column, formed by proliferation of the epithelium at the bottom of it, which subsequently becomes tubular, is as yet undecided.

CONGENITAL ABNORMALITIES OF THE EYEBALL.

In describing the numerous congenital abnormalities of the eyeball and its appendages, we propose first to speak of the more gross defects, in which the whole globe is involved; then, having dealt with those of the appendages, to proceed to the malformations met with in each individual structure of the eye.

ANOPHTHALMOS.

The term is applied to cases in which clinically no eyeball can be seen or felt (Fig. 1). Cases of this sort are rarely met with. Judging from the cases published, it would appear that it is more frequent to find the two eyes absent than only one. When only one eye is absent, the other not uncommonly presents some congenital defect. As a rule, patients who present this abnormality are born of healthy parents, and they themselves

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are healthy and well formed, being free from any malformations; though occasionally harelip, supernumerary digits, and other defects have been met with. The two sexes seem equally liable to this malformation. The lids are usually well formed, though small; sometimes they are adherent at their margins. The orbits, too, are often smaller than normal. The lacrymal gland is usually present, but the lacrymal puncta and canaliculi may be absent in one or both lids. Dissection has shown that in some of these cases a small rudimentary globe exists far back at the apex of the orbit, and that, strictly speaking, they are not cases of anophthalmos, but high degrees of microphthalmos. Ten cases are recorded, however,[1] in which not a trace of an eyeball or of anything representing it could be found in the orbit on dissection, and in which the optic nerve did not enter the orbit. In one it ended in the shape of a cone at the optic foramen, in another in a fibrous filament, and in five the chiasma was absent. What had happened, then, in these cases was this: no primary optic vesicle had budded out from the anterior primary encephalic vesicle, or, having budded out, it had failed to form a secondary optic vesicle. In one case the olfactory nerve was absent on one side, and in another case on both sides, together with one of the cerebral hemispheres; these structures are also expansions of the anterior primary encephalic vesicle. So it would appear that some disturbance affecting the development of the anterior primary encephalic vesicle is, at any rate, one cause of anophthalmos.

MICROPHTHALMOS.

Microphthalmic eyes may be divided into two classes:

1. Those in which there is no apparent congenital defect in the eye except the smallness of the globe.

2. Those in which, in addition to the eye being unusually small, there is some other abnormality, resulting from imperfect closure of the fœtal fissure.

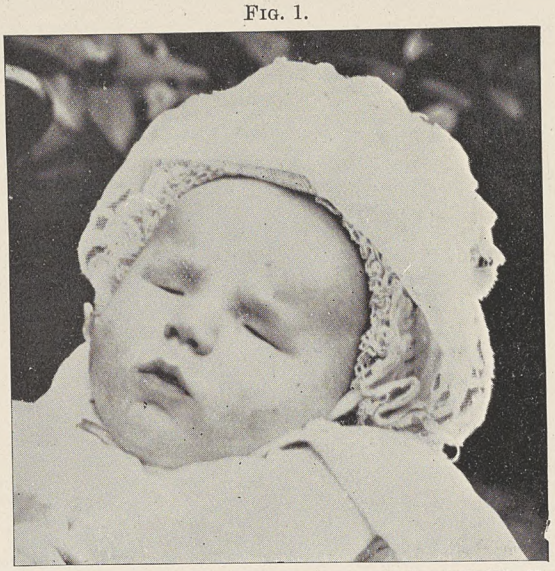
No very definite line can be drawn between highly hypermetropic eyes and those of the first class. Sometimes, when the central artery of the vitreous remains persistent and patent (as is described under the heading of Abnormalities of the Vitreous), the eyeball fails to develop to its normal size, though there has been perfect union of the fœtal ocular cleft.

The second class can be best treated under two heads,—viz., those where the defect in the closure of the ocular fissure is slight, and in which the eyeball retains nearly its normal shape, and those where the accompanying abnormality is very gross, the eye being usually exceedingly small, while connected with it are one or more cysts. (Figs. 2 and 3.) The subject of coloboma will be dealt with under the heading of Abnormalities of the Choroid. Here some description may be given of the rare cases in which cysts are met with in connection with rudimentary eyes. These patients are brought with cystic swell-

[1] Royal Lond. Ophth. Hosp. Rep., vol. xi. p. 429.

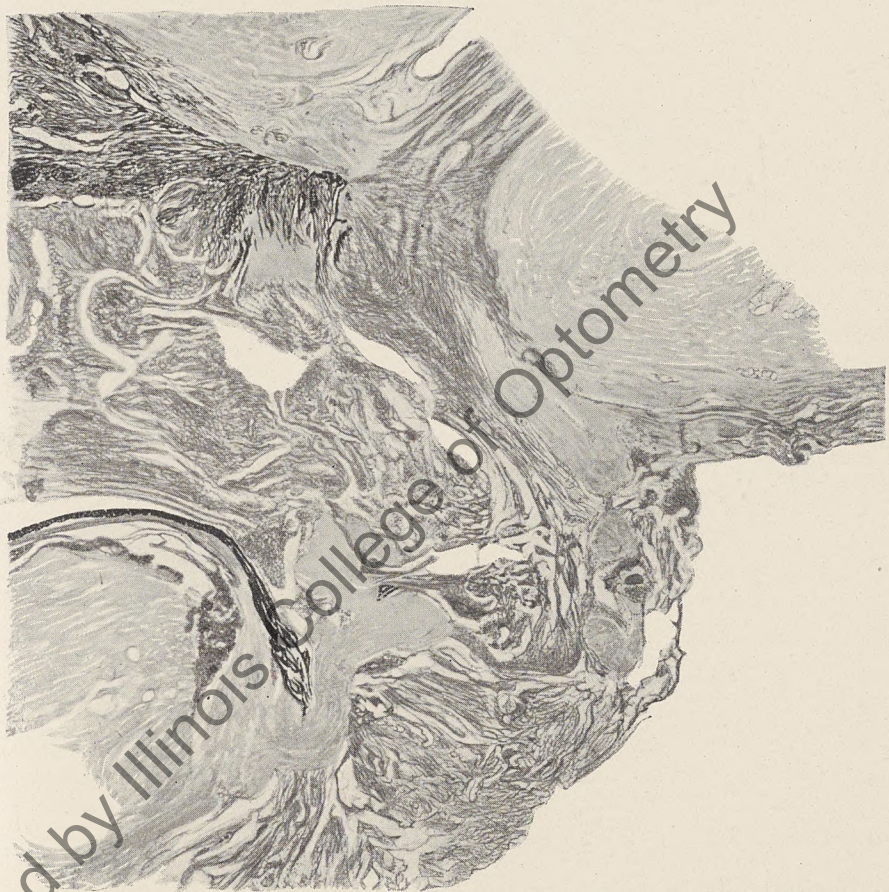
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FIG. 1.



Child, aged nine weeks, with congenital anophthalmos. (Royal Lond. Ophth. Hosp. Reports, vol. xi.)

FIG. 4.



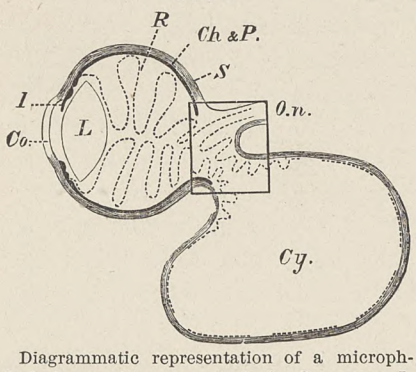
Portion of the eye represented in Fig. 2 included in the square, highly magnified. It shows the neck of the cyst, with retinal tissue passing through it from the eyeball into the cyst. (Royal Lond. Ophth. Hosp. Reports, vol. xii.)

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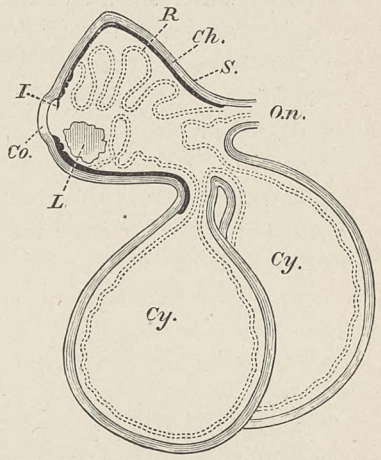
ings, sometimes of considerable size, situated in the lower part of the orbit or lower lid ; they are often very thin-walled and translucent. The skin of the lower lid stretched over them presents sometimes a bluish hue. The cyst may be so large as to fill the orbit and to all appearances replace the eyeball ; the small eyeball itself is usually situated far back near the apex of the orbit, and its presence or absence cannot be determined by clinical examination alone. It is this which has led to some of these cases being described

FIG. 2.



Diagrammatic representation of a microphthalmic eye with a cyst attached.—*Co*, cornea ; *L*, lens ; *I*, iris ; *R*, retina much folded ; *Ch* and *P*, choroid and pigment epithelium ; *S*, sclerotic ; *O.n*, optic nerve ; *Cy*, cyst lined by atrophied retina. The part marked off by straight lines is shown magnified in Fig. 4. (Royal Lond. Ophth. Hosp. Rep., vol. xii.)

FIG. 3.



Diagrammatic representation of microphthalmic eye with two cysts attached.—*Co*, cornea ; *L*, lens displaced and shrunken ; *I*, iris ; *S*, sclerotic ; *Ch*, choroid ; *R*, retina much folded ; *O.n*, optic nerve ; *Cy*, cysts lined by retina. (Trans. Ophth. Soc., vol. xiii.)

under the head of anophthalmos. Dr. Monacho[1] exhibited at the Catalonia Academy and Laboratory of Medical Sciences a little girl, aged thirteen months, the subject of this abnormality, in whom the cysts became tense during crying, and who was observed to press them frequently with her hands, and then to smile, a phosphene or subjective sensation of light being probably thus produced.

Dissection of these cysts reveals that they are connected, usually by a thin neck, with the small ill-developed eyeballs at their lower and posterior part, and that they are not separately formed cysts which have by their development checked the growth of the eye, as was supposed by some observers.

Considerable interest attaches to the composition of the walls of these cysts. All of them seem to have two coats,—an outer one of fibrous tissue continuous with the sclerotic, and an inner of more or less highly developed retina. (Fig. 4.) In a case examined by the authors,[2] the inner coat consisted only of bodies like those met with in the granular layers of the retina,

[1] Lancet, May 26, 1888.

[2] Royal Lond. Ophth. Hosp. Rep., vol. xii. p. 287.

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arranged in separate patches. In a case examined by Gallemaerts,[1] and in another examined by one of the authors (E. T. C.),[2] in which there were two cysts, it consisted of a continuous layer of branching cells and granular bodies. Rindfleisch[3] found the inner wall of a cyst composed of retina with its layers well developed, pigment epithelium, and an elastic lamina. The inner surface of the retina was directed towards the interior of the cyst. De Lapersonne and Czermak[4] also found fairly well developed retina lining the interior of cysts connected with microphthalmic eyes, but in their specimens the outer surface of the retina (that with rudimentary rods and cones on it) was directed towards the interior of the cyst. The following changes have been met with in the eyeballs to which these cysts are attached: opacity and vascularity of a small ill-developed cornea; coloboma of the iris; opacity of, calcareous deposit in, and displacement of, the lens; absence or only partial development of the vitreous; a folded, rucked condition of the retina, with imperfect differentiation of its layers; colloid bodies among the pigment epithelial cells on the inner surface of the choroid; an absence of the choroid in the region of the attachment of the cyst; nodules of cartilage in the fibrous tissue of the sclerotic, and a break in the continuity of this latter structure where it is continuous with the outer wall of the cyst.

The following theories have been put forward to account for the origin of these cysts:

Arlt[5] considers them to be due to increased intra-ocular pressure with stretching of the lower wall of the globe, weakened by the absence of choroid and partial defect of retina and sclerotic. Hess[6] accepts this explanation for some of his cases. Kundrat[7] describes the cystic formations connected with the lower wall of the eye as due to a projection of retinal tissue through the fœtal fissure into the mesoblastic tissue beneath the globe, this following on some defect in the development of the middle cerebral vesicle. Rindfleisch,[8] who examined a microphthalmic eye, with cyst attached, from a six to seven months' fœtus, which had hydrocephalus and the orbital roof pressed down so that it was convex below, thought that the alteration in the orbital roof compressed the globe, so bringing about a reopening and widening of the choroidal cleft and an intrusion of the retinal tissue into the surrounding mesoblast. De Lapersonne, to account for the position of the retina mentioned above, suggests that it had become secondarily detached and convoluted; that one of these folds facing the ocular cleft had become pushed into it, perhaps by a fluid analogous to that contained in retinal cysts, and, yield-

[1] Kyste congénital de la Paupière avec Microphthalmos. Bruxelles, 1893.
[2] Trans. Ophth. Soc., vol. xiii. p. 114.
[3] Archiv für Oph., Bd. xxxvii., Abth. 3, S. 192.
[4] Archives d'Oph., t. xi. p. 207.
[5] Anzeiger der k. k. Gesellschaft der Aerzte. Wien, 1885, No. 17.
[6] Archiv für Ophth., Bd. xxxvi., Abth. 1, S. 135.
[7] Wiener Medizin. Blätter, Nos. 51, 52 (1885), and 53 (1886).
[8] Ibid.

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ing to this pressure, was invaginated like a glove-finger and forced outward into the cellular tissue of the orbit.

The retina in the human fœtal eye is normally in a folded condition, and it seems possible to imagine that if there was some delay in the closure of the ocular cleft and in the development of the vitreous, the mere continued growth of the retina would tend to make it protrude through the cleft.

BUPHTHALMOS, HYDROPHTHALMOS CONGENITUS, OR CONGENITAL GLAUCOMA.

The condition of the eye which has received the above names is best spoken of as congenital glaucoma; for the peculiar appearances which are produced are all the result of increased tension in an eye the cornea and sclerotic of which are thin and extensile, and which have not become tough and inelastic as they do in later life. The cornea in this disease is considerably enlarged; occasionally there are nebulæ in its centre, and sometimes the opaque white tissue of the sclerotic is prolonged into it for a short distance at the margins. The sclerotic is much thinned, and the pigmented tissue of the ciliary body shows through, giving it a dull bluish appearance. The curvature of the cornea and sclerotic is altered, so that the front of the globe has a more globular shape than normal; the whole appearance is very much that of an ox's eye; hence the name buphthalmos. The anterior chamber is generally deep, but in a few cases it is absent altogether, the entire anterior surface of the iris being in contact with the cornea. The iris is much stretched, and often tremulous; the lens in some cases is mobile, swaying backward and forward on movement of the globe. The tension, as a rule, is found to be increased; occasionally cases are met with in which the tension is increased and the globe enlarged, but in which after a time spontaneous arrest of the disease seems to occur, the tension for the remainder of life being normal and the vision not further deteriorating. The refraction is usually myopic, but the amount of myopia is not such as might have been expected from the increased lengthening of the globe. The optic nerve is always deeply cupped.

It is easy to understand that increase of tension will cause the elastic coats of an infant's eye to expand more than those of an adult; but what does at first seem difficult to explain is, why the anterior chamber should be deep, and why some of the cases go on to spontaneous cure; for in primary glaucoma of adults the anterior chamber is, as a rule, shallow, and no amelioration of the symptoms occurs, if treatment is not resorted to.

The primary block to the circulation of fluids in the eye in primary glaucoma is now generally believed to be at the circumlental space, an obstruction being thus occasioned to their passage forward from the vitreous into the posterior and anterior chambers; consequently the iris and lens are pressed forward and the anterior chamber is made shallow. If the primary block was situated, not at the circumlental space, but at the angle

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of the anterior chamber, then fluid would collect in the anterior chamber, and instead of its being made shallow it would be deepened.

In the article on congenital anterior synechia it is shown that, through a failure in the separation of the anterior fibro-vascular sheath from the back of the cornea, a congenital adhesion of the iris to the cornea may result. Such an adhesion situated at the periphery of the chamber, in the region of the ligamentum pectinatum, would prevent the passage of fluid into the spaces of Fontana. In several buphthalmic eyes examined microscopically by one of the authors, an adhesion of the periphery of the iris to the cornea was found. It is by some supposed that it is not possible to have a deep anterior chamber and at the same time to have its angle closed by an adhesion of the root of the iris to the cornea; but in these eyes this is constantly found to be the case, an abrupt bend occurring in the iris at the point where the adhesion ceases. It can easily be understood how, as the globe enlarged and the anterior chamber deepened, any adhesions between the periphery of the iris and the cornea would become stretched, and might possibly give way, or at any rate be so attenuated as to cease to cause any obstruction to the exit of the aqueous humor; in such cases a spontaneous cure would occur. It is, then, probable that congenital glaucoma is due to the iris failing to become separated from the back of the cornea at the periphery of the anterior chamber, and that the adhesions which are thus left may in some cases, as the eye enlarges, become much stretched and even give way, and a normal tension be established.

MULTIPLE EYES AND CYCLOPIA.

Such strange malformations as the occurrence of more than two eyes, or the presence of only one central eye (cyclopia), are met with in monsters, and may be studied in teratological specimens. Parts ending in free extremities at times bifurcate; such a condition in the case of the digits leads to supernumerary fingers and toes. This tendency to bifurcation may, however, affect the trunk; when it affects the head end it is spoken of as anterior dichotomy; when the opposite end, as posterior dichotomy. There may be various degrees of anterior dichotomy. Thus, one body may have two completely separate heads, and then, of course, there would be four eyes. Or the two heads may be partially joined, when, if the two median orbits are quite distinct, there will still be four eyes. If the two median orbits are fused together, the two median eyes may be joined to a various extent: sometimes the globes are united only posteriorly, and the two corneæ are quite distinct; in others one large globe is formed, the eyelids of the median eyes or eye become united, and, having no inner commissures, bound a single fissure. Posterior dichotomy of the axis may extend forward into the basisphenoid region and an accessory face be produced. In the Royal College of Surgeons Museum there are two specimens of fœtal pigs showing this condition. In one, the two eyes of the accessory face are fused together as far as the edges of the irides; in the other, the eyes of the accessory face are

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distinct, but so obliquely placed that the fissures of the eyelids are almost vertical. There is also a female human fœtus similarly affected, in which there are four eyes, but the inner ones are contained in a single orbit. The presence of only one central eye (cyclopia) is due to a deficiency of the axis in the facial region. The two orbits and the two eyes forming the two sides become fused into one. The extent of the fusion of the two eyes into one varies considerably; a frontal proboscis is always present.

CRYPTOPHTHALMOS.

This is the name which has been given to a very rare condition, in which there is complete absence of the eyelids and palpebral fissure, and where the skin passes continuously from the brow over the surface of the globe (which can be seen moving beneath it) to the surface of the cheek. The case of a child exhibiting such a malformation has been published by Zehender,[1] with an anatomical description of the condition by Manz. He found that all the appendages belonging to the lids were absent,—viz., eyelashes, lacrymal gland, and lacrymal ducts; only the muscle existed. On the left side there was a well-developed orbicularis; on the right only part of it could be found. The skin extending over the eyes was connected with its surface by a subcutaneous cellular material, and not limited by a closed cavity.

Van Duyse[2] has described a similar case,—a child three weeks old, who had, in addition, other abnormalities; among them imperfect development of the parietal bone, and meningo-encephalocele.

CONGENITAL ABNORMALITIES IN THE OCULAR APPENDAGES.

EYEBROWS AND ORBIT.

The eyebrows may vary in shape, size, and color. Cases have been observed of complete absence of the eyebrows and eyelashes. Patches of white hair in a dark brow—piebald eyebrows—are sometimes seen. In albinos the eyebrows and eyelashes are quite white; the latter thin, long, and silky.

Dermoid cysts in connection with the eyebrows or the lids are by no means uncommon; they have been met with deeply situated in the orbit, in which case it is very difficult to diagnose them from other orbital growths, and also to remove them completely. These dermoid cysts occur in the course of the fœtal orbito-nasal fissure, and are most frequent at the outer angle of the brow. They lie beneath the orbicularis muscle and in contact with the pericranium of the frontal bone, which may be hollowed out under them. To the touch they feel firm, smooth, and rounded, and they roll beneath the finger on the bone. They vary in size, but are not often much larger than a cherry. Dermoid cysts at the inner angle of the orbit are

[1] Proceedings of Fourth International Ophthalmological Congress, p 86.
[2] Annales d'Oculistique, 1889, t. x. p. 69.

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more rarely met with; a connection may exist between them and the dura mater,—a circumstance which it is well to bear in mind in order that they may not be confused with meningoceles.

Power[1] recently recorded the case of an infant with microcephalus, in which the orbits were extremely small, measuring only two and one-half centimetres from the inferior border to the foramen opticus; their floors were horizontal and their roofs almost vertical. The eyes naturally were exceedingly proptosed.

Epicanthus is a name which was first applied by von Ammon to a condition in which there is an excess of skin between the two eyes about the root of the nose, so that crescentic folds of it overlap the inner canthi and part of the palpebral aperture. It is generally due to some defect in the development of the bridge of the nose. In the Mongolian race, who have no bridges to their noses, slight epicanthus appears to be the normal condition. Among European children, before the bridge of the nose develops, a tendency to it is frequently seen, which disappears as they grow older. One of the most frequent causes of defect of development of the bridge of the nose is congenital syphilis: hence, as might have been expected, a history of this affection can frequently be obtained in cases of epicanthus.

Epicanthus is sometimes associated with congenital ptosis. In severe cases the fold of skin may extend as far over the eye as the inner margin of the cornea; the patient then appears very much as though he had an internal squint. Frequently a mother brings her child complaining that it squints, when really it has epicanthus.

CONGENITAL ABNORMALITIES OF THE LACRYMAL APPARATUS.

Malformations of the Canaliculi.—These are the commonest forms of abnormalities met with in connection with the lacrymal apparatus. The canaliculi are sometimes represented by a groove the edges of which have failed to become united in the ordinary way, or the edges of the groove may have united in only a part of their extent; there are then two openings into one canaliculus. Occasionally one or more of the canaliculi may be completely absent, or one or more of the puncta may not be patent. Steffan[2] has described a patient who had a second punctum a line below and to the outer side of the normal one; it was uncertain whether it opened into the sac or into the other canaliculus.

In several cases of anophthalmos, defects of the canaliculi have been met with.

Fistula of the Lacrymal Sac.—Defects in the closure of the groove which ultimately develop into the lacrymal sac and duct are exceedingly rare. Cases of it have been recorded by G. Beer, Scarpa,[3] Hartridge,[4]

[1] Trans. Ophth. Soc., vol. xiv. p. 212.
[2] Klin. Monatsblatt, 1866, S. 45.
[3] Traité complet d'Ophthalmologie, vol. iv. p. 1103.
[4] Trans. Ophth. Soc., vol. xii. p. 172.

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Agnew,[1] and Casey Wood;[2] in all of which the opening into the lacrymal sac was exceedingly small, and symmetrical on the two sides.

Stricture of the Lacrymal Duct.—Cases of this are sometimes met with as a congenital defect.

Malformations of the Caruncle.—The caruncle may be the seat of two forms of congenital growth: both are very rare. 1. There may be small dermoid tumors, of which an excellent example is pictured by Demours,[3] with hairs growing from it. Microscopically, these growths are seen to be precisely similar to the dermoids met with so much more frequently at the sclero-corneal margin. 2. There may be small vascular growths of a bright-red color, microscopical sections of which show numerous thin-walled blood-vessels cut in various directions, with a small quantity of loose fibrous tissue between them.

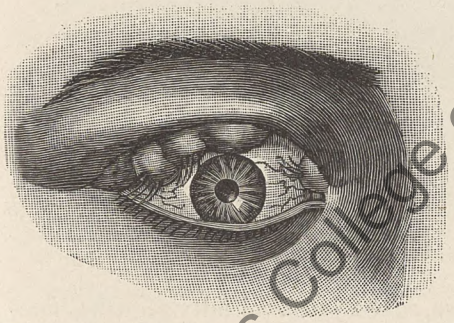
Abnormalities of the Lacrymal Gland.—Morton[4] has recorded the case of a girl, aged six, who never shed any tears with her right eye, though they flowed copiously from the left whenever she cried.

The secretion of the lacrymal gland has also been noticed to be absent in some cases of anophthalmos. It must be borne in mind that absence of the lacrymal secretion does not necessarily imply absence of the gland. No child sheds tears during the first few days of life; and it is quite possible that, though the gland were present, its function might never be established.

EYELIDS.

Both eyelids may be congenitally absent; the conjunctival sac then fails to develop, and the front of the eye remains covered with skin. This condition has already been spoken of under Cryptophthalmos.

FIG. 5.



Double congenital coloboma of the right upper lid in a boy aged twelve years.

Coloboma of the Eyelid.—A large portion of one of the eyelids may be congenitally absent, or the lid may be divided into two parts by a fissure of greater or less extent: such cases are spoken of as colobomata of the eyelid.

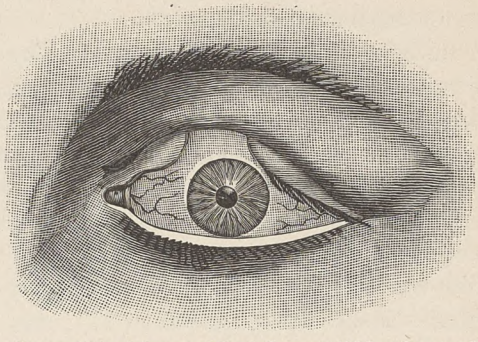
Dor[5] and Nicolin collected forty-six recorded cases of this abnormality, and twelve of oblique fissures of the face, accompanied by partial coloboma of the lid. Of the forty-six cases, twenty-seven

[1] Trans. Am. Ophth. Soc., 1874, p. 209.
[2] Arch. of Ophth., vol. xxii. p. 25.
[3] Maladies des Yeux, 1818, pl. lxiv., fig. 1.
[4] Trans. Ophth. Soc., vol. iv. p. 350.
[5] Revue Générale d'Ophth., 1888, p. 529.

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had only one lid affected, two had the same eyelids of the same eye, sixteen had one lid of each eye, and one had all four lids involved. The gap in the lid is usually situated to the inner side of the middle line, and when a portion of the lid is absent it is usually the inner part of the upper one. The defect may extend from the palpebral to the orbital margin (Figs. 5 and 6), or only be a small indentation of the free border of the lid. (Fig. 7.) The shape of the gap left is either triangular or quadrate; when the former, the base of the triangle is at the free margin of the lid.

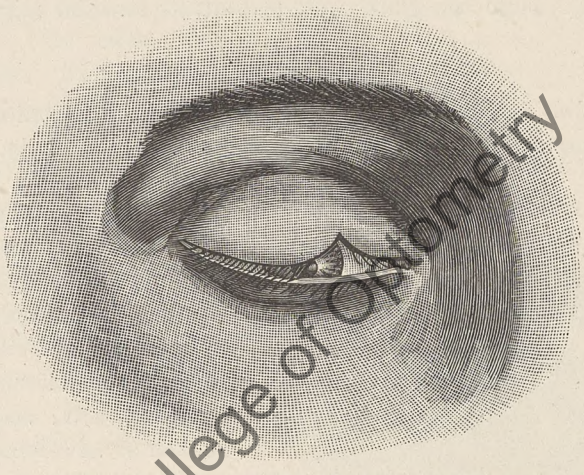
FIG. 6.



Congenital coloboma of the left upper lid in a boy aged two years.

This abnormality is often found associated with other congenital defects,

FIG. 7.



Small congenital coloboma of the right upper lid in a girl.

such as dermoid growths of the cornea, subconjunctival fatty growths, hare-lip, cleft palate, and supernumerary auricles.

Nicolin and Dor have offered the most probable explanation of its cause. They consider it to be due to an imperfect closure of the oblique facial fissure, the persistence of the upper end of which causes the lid to develop in two parts.

Anchyloblepharon, or adhesion of the lids, might have been expected to be a more common congenital anomaly than it is, seeing that the edges of the lids are united during several months of fœtal life. This adhesion,

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however, is only a cementing together of the epithelium. In anchyloblepharon the adhesion is composed of vascularized tissue; it is probable that it results from an inflammation of the margins of the lids while they are in contact. It has been met with in several of the cases recorded under the name anophthalmos.

Symblepharon, or adhesion of the eyelid to the globe of the eye, is exceedingly rare as a congenital affection.

Lagophthalmos and Congenital Shortness of the Lid.—Incomplete closure of the palpebral fissure when the lids are shut is spoken of as lagophthalmos. When this condition is congenital, it is due to an abnormal shortness of the upper lid. The lids can be brought together by a strong contraction of the orbicularis muscle, but on gentle closure a gap is left; they remain also separated during sleep, but the cornea is not exposed, for on shutting the lids the eyeball rolls upward.

Many varieties exist in the size and direction of the palpebral aperture, constituting racial peculiarities which need not be treated of here. An abnormal smallness of the palpebral aperture—blepharophimosis—is common in cases of microphthalmos and anophthalmos.

Congenital Growths of the Eyelids.—The lids may be the seat of congenital growths, such as moles, nævi, and cysts. The nævi may be either lymphatic or vascular. Both forms tend to increase in size after birth. Lymphatic nævi are rare; at times they are very large, extending into the orbit and involving the conjunctiva.

The vascular nævi may be superficial or deep, and telangiectatic or cavernous. A further description of them is not necessary in this article.

Dermoid cysts of the eyelids, and cysts in connection with microphthalmic eyes, which extend into the lower lid, have already been treated of.

Ectropion of the eyelid is an exceedingly rare congenital affection. It has been met with in a few cases associated with other congenital abnormalities affecting the eye, such as microphthalmos (von Ammon) and buphthalmos (Marcus Gunn).

Congenital entropion and trichiasis are more frequently met with; several examples of the latter, affecting the lower lid, are recorded in a recent paper by Sydney Stephenson.[1] They have been attributed to inflammation and to defective development of the tarsus.

CONGENITAL DEFECTS OF THE MOVEMENTS OF THE EYE AND EYELIDS.

Ptosis, or drooping of the upper lid, is a common congenital affection; it is almost always bilateral, and is met with in very various degrees. In the most complete cases patients present a very characteristic appearance. Besides the drooping of the lids and the obliteration of the palpebral folds, the forehead is much wrinkled, due to the contraction of the anterior portion of the occipito-frontalis muscle, which tends slightly to raise the lids. The

[1] Trans. Ophth. Soc., vol. xiv. p. 13.

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head is also thrown back and the eyes are rotated down, by which means, when the patient is looking straight forward, a portion of the pupil is brought opposite the palpebral aperture.

Of the ocular muscles, the internal recti are the most frequently affected. The superior, inferior, and external recti and the superior oblique have also been found at fault. Often two or more muscles are found affected on the same side. Congenital ptosis and congenital defect of the superior rectus not uncommonly go together. The subjects of these anomalies do not, however, usually present any malformations in other parts of the body. In many of them it has been observed that the optic axes were not parallel, but in none was diplopia a symptom.

The condition is not infrequently hereditary. It is generally due to a developmental defect of the muscles; in a few exceptional cases in which there were gross changes in the nervous system it was attributed to an anomaly of the nerves supplying the muscles.

The muscles may be either completely absent, badly developed, too short, or inserted at an unusual position on the globe. (Henck[1] and Lawford.[2]) It is not always possible to diagnose the precise nature of the defect from the movements of the globe.

Nystagmus, or an oscillatory movement of the two eyes, is commonly met with in cases in which there is a congenital defect of the sight. It is very common in connection with congenital cataract and albinism. The movements of the eyes vary very much in direction and in rapidity in different cases. By far the most usual direction for the motion to occur in is from side to side; it may, however, be vertical from above downward, or rotatory; sometimes rotation is combined with a lateral motion. The rapidity with which the eyes move may be so great that the outline of the corneæ can barely be distinguished, or it may be a slow, twitching, and easily overlooked motion. In congenital nystagmus, though the eyes are moving, the patient never complains that the object to which his vision is directed does not appear stationary.

CONGENITAL ABNORMALITIES OF THE CONJUNCTIVA.

The conjunctiva may be the seat of certain congenital growths. The most frequent of these are the dermoid tumors, which may be partly corneal and partly conjunctival; they are dealt with at length under the abnormalities of the former structure. Congenital growths very similar to these dermoids in structure, and sometimes associated with them, are met with in the outer angle of the upper conjunctival cul-de-sac; they are spoken of as subconjunctival fatty growths. When small, they remain concealed beneath the upper lid; when large, they project into the palpebral fissure. Microscopically, the epithelium over them is found thick and laminated, and the

[1] Centralblatt für Augenheilk., 1881, S. 335.

[2] Trans. Ophth. Soc., vol. viii. p. 262.

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mass itself is seen to be composed of fibrous and fatty tissue. Pigmented patches similar to the moles of the skin are occasionally met with in the conjunctiva; most often in persons who have multiple moles of the face. They must be distinguished from the congenital pigmentation of the sclerotic which is so frequent in some animals that it may be considered the normal condition, and in man is not an uncommon abnormality about the seat of the anterior perforating arteries.

The other forms of congenital growths met with in connection with the conjunctiva are nævi, vascular and lymphatic, and tumors composed of well-developed bone-tissue, which belong to the class of teratomata; they are usually situated beneath the conjunctiva, between the outer margin of the cornea and the external canthus.

CONGENITAL ABNORMALITIES OF THE CORNEA.

The cornea may be congenitally defective as regards its transparency, its size, and its shape. It may also be the seat of a congenital fleshy growth.

OPACITIES OF THE CORNEA.

A congenital opacity of the cornea may be complete or partial. In many of the cases of complete opacity, as in some recorded by Farar,[1] the cornea is enlarged, and not only the cornea, but the whole globe, constituting the condition termed congenital hydrophthalmos or buphthalmos, which has already been described. Complete opacity of the cornea is also met with in connection with microphthalmos. In two cases of this sort which we examined microscopically we found that the anterior elastic lamina was absent, and that the anterior layers of the cornea did not present their usual laminated arrangement, but crossed each other in an irregular way, whilst coursing among them were numerous blood-vessels.

Partial congenital opacities of the cornea present various degrees of intensity, sometimes being densely white at other times only a faint haze. They may be situated in any part. Two forms which present special characteristics have had names applied to them. One of these is dense white in color and situated at the corneal margin, looking as though a portion of the sclerotic had been prolonged inward into the cornea: Keiser termed it *sclerophthalmos*. The other is a ring of opacity situated in the periphery of the cornea, closely resembling an arcus senilis; the ring, however, is usually more complete than in the latter. The condition looks very like microcornea, with which it is sometimes associated. It may be distinguished from it by the presence of a diaphanous ring between the margin of the cornea and the opacity. Wilde[2] speaks of it as *arcus juvenilis;* Sybil, as *macula arcuata.*

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[1] Medical Communications, vol. ii. p. 463, 1790.

[2] Malformations and Congenital Diseases of the Organs of Sight, 1862.

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VARIATIONS IN SIZE OF THE CORNEA.

The cornea is enlarged (macrocornea) in buphthalmic eyes; it is frequently abnormally small (microcornea) in microphthalmic ones. It also sometimes has less than its normal diameter in eyes otherwise perfectly healthy.

CONICAL CORNEA.

The cornea may be altered so that, instead of presenting its usual curvature, it becomes dome-shaped or conical; the apex of the cone may be in the centre, but usually it is a little below. Dissection of such eyes has shown that the substance of the cornea is thinned in that situation. (Middlemore,[1] Hulke.[2])

Some cases of conical cornea are certainly congenital, though in many the defect does not appear until adult life. Tweedy,[3] however, holds that in these cases also there is some latent embryological defect which predisposes the cornea to alter its shape in the way it does.

DERMOID GROWTHS OF THE CORNEA.

Fleshy growths of the eye may be divided into two classes: those which are entirely confined to the globe, and those in which a cuticular band passes between the surface of the globe and the brow or some other part of the face.

The first variety are situated generally at the lower and outer margin of the cornea, springing partly from the cornea and partly from the sclerotic. They are most often single, and present in one eye only; they may, however, be symmetrically placed on the two eyes, or one eye may have two tumors, one on each side of the cornea. Their size is very variable: they are sometimes smaller than the head of a pin, at other times they are so large as to protrude between the lids and prevent their closure. They are often small at birth and enlarge about puberty; it is at this period of life that the surgeon is most often consulted respecting them, partly because their increase in size renders them more conspicuous, and partly because at this time hairs frequently commence to grow from them which give rise to some conjunctival irritation. Wardrop[4] describes a case in which upwards of twelve long and strong hairs grew from the middle of the tumor and, passing between the eyelids, hung over the cheek. These hairs did not commence to appear until the patient reached his sixteenth year, at which time also his beard began to grow.

Dermoid tumors on the eye may be conical, flat, or pedunculated; they usually have an oval base, the long axis of which always corresponds with the palpebral aperture. They are firm in consistence and of a yellowish-

[1] Treatise on Diseases of the Eye and its Appendages, vol. i. p. 532.
[2] Royal Lond. Ophth. Hosp. Rep., vol. ii. p. 155.
[3] Trans. Ophth. Soc., vol. xii. p. 67.
[4] Morbid Anatomy of the Human Eye, 1834.

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pink color; fine blood-vessels are sometimes visible on their surface. They have been met with in dogs, horses, oxen, and sheep, as well as in man. A specimen contained in the Royal College of Surgeons of England shows one in a sheep's eye, from which a tuft of wool is sprouting.

The second form of dermoid growths of the eye is much less common than the first; among the few which have been recorded may be mentioned those of van Duyse[1] and Polaillon,[2] in which a fleshy band passed from the surface of the cornea downward and inward to the skin at the margin of the inner commissure. In a case of Manz's there was a coloboma of the lid upward, and a band presenting all the characters of skin stretched from the brow to the cornea. Burns[3] described a fœtus in which two cuticular bands passed from the centre of each cornea and joined into a larger one, which ended in a broken extremity. Picqué[4] found that out of ninety-four cases of dermoid growths of the eye twenty-seven were complicated with some other abnormality. The most important and most frequent of these was coloboma of the lid. When a dermoid tumor exists in association with coloboma of the lid, it is found that it corresponds to the gap in the latter, so that when the lids are closed it exactly fills it. The other complications that have been met with are: of the eye, microphthalmia and coloboma of the iris and choroid; of other parts of the body, preauricular tumors, macrostoma, hare-lip, absence of the external auditory meatus, and syndactylism. Microscopically, dermoid growths are seen to be composed of fibrous tissue often mixed with adipose tissue; this is covered by laminated epithelium, the surface cells of which are scaly and devoid of nuclei, like those on the skin, and unlike those on the surface of the cornea and conjunctiva. Hair-follicles, sweat-glands, and sebaceous glands are met with, also glands similar in character to the glands of Moll, in the eyelid. Blood-vessels course through the growths, and nerves have been demonstrated in them. Several explanations of the mode of formation of these dermoid growths of the eye have been offered. The epibulbar variety is, we think, best explained by the theory put forward by Rhyba.[5] He pointed out that on all parts of the surface of the body which remain exposed skin is formed, and that when a part becomes covered, as the eye is by the lids, a mucous membrane is developed. He believes that when a dermoid growth occurs in consequence of imperfect or delayed closure of the lids, a portion of what should be conjunctiva remains exposed and assumes the character of skin. The cases in which cuticular bands are formed are probably due, as suggested by van Duyse, to adhesions forming between the inner layer of the amnion and the surface of the embryo.

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[1] Ann. Soc. Méd. de Gand, 1882, p. 141.
[2] Bull. de la Soc. Anat., 1874, p. 12.
[3] Handb. der Prakt. Chir., vol. i. p. 262, 1859.
[4] Anomalies de Développement et Maladies congénitales du Globe de l'Œil. Thèse, Paris, 1886, pp. 356–420.
[5] Prager Vierteljahrschrift, vol. x. p. 3, 1853.

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CONGENITAL ABNORMALITIES OF THE IRIS.

The iris may vary as to its color and present congenital defects in the condition of the pupil, in the persistence of a portion of the pupillary membrane, in being tremulous (iridodonesis), and in a deficiency of the whole (irideremia) or part of its structure (coloboma).

VARIATIONS IN THE COLOR OF THE IRIS.

The iris presents many variations with regard to its color. Pigment is located in it in two parts: (1) in the epithelial layers on its posterior surface; (2) in the branching cells of its stroma, chiefly those in the anterior part. When no pigment is present in this latter position the iris is blue, when only a slight amount it is green, and when in large quantities brown, or even almost black in the negro races. Absence of pigment from the epithelial layers is always associated with absence of pigment in the stroma and in the other parts of the body where it is usually present, constituting the condition known as albinism. Pigment is deposited in the epithelial layers very early in fœtal life, but does not make its appearance in the mesoblastic tissue of the iris until after birth. The iris tissue at this time is very thin, and for these two reasons all babies' eyes are for the first few weeks after birth of the same grayish hue. Irregularities may occur in the deposition of pigment in the iris, sometimes only temporary, at other times persisting throughout life. A sector of the iris may remain blue, whilst the rest of it is brown; or patches of brown may be scattered about in a blue iris, forming what is termed a piebald iris. In some individuals the irides of the two sides are of different colors (heterochromia). W. G. Sym[1] has shown that when this is the case the parents of the individual are usually of different complexion. His cases also seem to show a greater liability of the blue over the brown eye to disease.

Little, dark, raised patches are occasionally met with in the iris comparable to moles of the skin. Microscopically, they are found not to be simply a deeply pigmented patch, but to consist also of a group of round and branching cells. They are liable to be the starting-points of a melanotic sarcoma, but this is a very rare disease of the iris.

Congenital darkly pigmented nodules at the pupillary margin of the iris are sometimes met with, due to extension forward to an abnormal extent of the two layers of uveal pigment which line its posterior surface. Such an extension forward of the pigment epithelium is the normal condition in the horse's eye. The condition is termed ectropion of the uveal pigment. A good case of it is pictured and described by Wicherkiewicz.[2]

Complete or nearly complete absence of pigment from the eye occurs, as has been stated, in connection with absence of pigment from other parts

[1] Ophth. Review, vol. viii. p. 202.
[2] Archiv für Ophth., Bd. xxxvii., Abth. 1, S. 204.

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of the body, in the condition known as general or universal albinism, and persons so affected are spoken of as albinos. In them the skin has a peculiar pinkish-white, transparent appearance; the hair may be perfectly white or of a faint straw color; sometimes there is a fine, white, downy hair all over the body. The eyelashes are long, fine, white, and silky. The eyes appear pink, a red reflex being seen from the pupil in ordinary daylight. This is due to the non-absorption of light by the retinal epithelium on account of the absence of pigment in it, and to light entering the eye through its tunics. A pinkish color is often seen through the iris tissue, which in these cases is generally of a grayish hue. The excess of luminous rays entering the eye leads to defect of vision and intolerance of light by the retina; consequently, individuals thus affected are found invariably to screw up the eyes and to go about, especially in a bright light, with their lids half closed. They frequently have nystagmus, or oscillation of the eyes, and are usually amblyopic.

Ophthalmoscopically, owing to the absence of the pigment, the ramifications of the choroidal blood-vessels are well seen.

Little is known as to the cause of albinism. It is sometimes hereditary; several children of the same parents may be affected, or it may affect members of different generations. It is also found more frequently in some races of mankind than in others; it is common among negroes. Insalubrious conditions of climate and hygiene are supposed to favor its development. It is met with very frequently in such parts as the west coast of Africa.

ABNORMALITIES OF THE PUPIL.

The pupil may present several congenital abnormalities. It may be altered in its position (corectopia); in its size, being abnormally small (microcoria); in its shape (discoria); and, finally, instead of one pupil there may be several (polycoria).

Corectopia.—It is by no means infrequent to find the pupil in one or both eyes slightly excentric, but the more extreme cases of corectopia are only rarely met with; these are often associated with ectopia of the lens. A displaced pupil is frequently small, inactive, and sometimes not regularly circular. The direction in which it is displaced is usually upward and outward.

Microcoria.—As just mentioned, a displaced pupil is frequently small; other cases of microcoria are the result of fœtal iritis and the formation of posterior synechiæ. A pupil may be of the normal size and yet not dilate well on the application of a mydriatic; such a condition is not uncommonly associated with congenital cataract.

Discoria, or abnormality in the shape of the pupil without any absence of the iris tissue, may, like microcoria, be the result of posterior synechiæ following fœtal iritis. It may also occur from persistence of portions of the pupillary membrane; sometimes from this cause the margin of the pupil is toothed and the pupil itself is star-shaped. (Fig. 9*a*.)

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Polycoria, or the condition in which there is more than one opening in the iris, is but seldom met with. No well-authenticated case has been recorded in which more than one opening surrounded by a sphincter muscle existed, though there are several in which the size of the additional openings was affected by myotics and mydriatics, due to the contraction or dilatation of the sphincter surrounding the normal pupil altering the condition of the adjacent iris.

Cases of polycoria may be divided into the four following distinct classes:

1. Those in which the normal pupil is divided into two by the persistence of a band of the pupillary membrane. A good example of this variety has been figured by Wilde, in which a band passing vertically across the normal opening produced a figure-of-eight pupil, both sections of which acted to light.

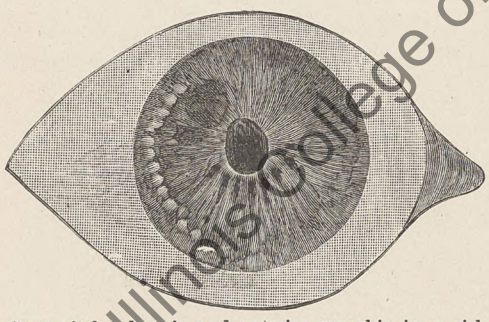
2. Cases which may be termed "coloboma with a bridge,"—that is, cases of complete or partial coloboma of the iris in which a band of tissue, probably a portion of the pupillary membrane, stretches across the opening and divides it into two. Examples of this are recorded by von Ammon and Saemisch.

3. A variety of which Mittendorf[1] has described two cases, father and daughter. One of them had in one eye five pupils,—the central normal one, which was oval, and four others, situated at the periphery of the iris, conical in shape, with their bases at the margin of the cornea. The other had in one eye a central pupil, and below it at the periphery of the iris a large opening divided into two by a thin vertical band of tissue.

They might be termed cases of congenital iridodialysis. Talko has recorded one somewhat similar, in which numerous posterior synechiæ were present.

4. Those of which Fig. 8 represents a good example. In it there were as many as nine openings in the iris,—the normal pupil, and below and to one side of it eight smaller, somewhat triangular openings. These appeared to be situated just external to the outer border of the sphincter muscle, and looked like gaps left between the radiating fibres of the iris.

FIG. 8.



Congenital polycoria and anterior synechia in a girl aged three and a half years.

The child, at the time the drawing was made, was three and a half years old; the defect, however, had been noticed soon after birth; its other eye was normal. At the periphery of the left iris, on the outer side,

[1] Trans. Am. Ophth. Soc., vol. iii. p. 735.

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were several little white projections from its anterior surface; these seemed to be attached to the back of the cornea.

Cases similar in character to this have been recorded by Rumschewitsch, Baudry, and de Schweinitz.

PERSISTENT PUPILLARY MEMBRANE.

The formation of the pupillary membrane from the anterior fibro-vascular sheath of the lens has been described at the commencement of the article. In man it usually completely disappears before birth; persistence of a portion of it is one of the commonest congenital abnormalities of the eye.

Franke[1] found remnants of it in thirty-two patients out of three thousand five hundred and eight, or 0.9 per cent.; in eighteen only filaments

FIG. 9.

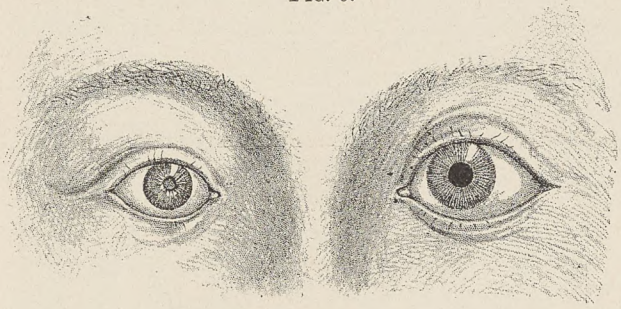
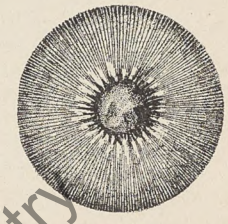


FIG. 9*a*.



Congenital microphthalmos and cataract, with persistence of numerous tags of pupillary membrane, in a girl aged eight months. Fig. 9*a* represents the iris of the right microphthalmic eye magnified.

were present, and in fourteen a membrane. Three cases had remnants in both eyes. It occurred in the ratio of seven cases in the right eye to five in the left, and in the female sex in the ratio of nineteen to thirteen in the male.

Stephenson[2] gives a higher percentage than this. Out of a total of three thousand four hundred and fourteen eyes he detected vestiges of pupillary membrane no less than sixty-eight times, or in 1.7 per cent. of the cases examined. In thirteen of the sixty-eight cases there was persistent pupillary membrane in both eyes. Of the monocular cases, the right eye was the seat of the anomaly in twenty-five instances, and the left eye in the remaining seventeen. As regards sex, the percentage among nineteen hundred and ninety-four males was 1.81, and among fourteen hundred and twenty females 2.25.

When persistent, the pupillary membrane varies in extent, in color, and in its relation to surrounding structures. Fibres of the pupillary

[1] Archiv für Ophth., Bd. xxx., Abth. 4, S. 289.
[2] Trans. Ophth. Soc., vol. xiii. p. 139.

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membrane are distinguished from posterior synechiæ due to iritis by arising from the anterior surface of the iris, from the corona or smaller circle.

Cases have been recorded by van Duyse in which fibres arising from the small circle of the iris have converged towards the centre of the pupil and there united into a true membrane. More often no true membranes exist, only fibres being present. These fibres may be arranged in several different ways.

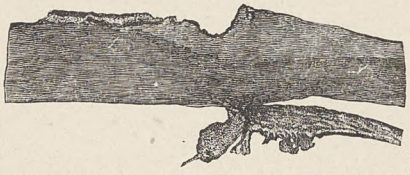
1. Several fibres arising at different points in the circumference of the small circle of the iris stretch across the pupil and form a delicate network in front of it.

2. Fibres run tangentially between two points in the small circle of the iris.

3. All the toothed projections of the small circle are prolonged inward and project beyond the pupillary margin. (Fig. 9.)

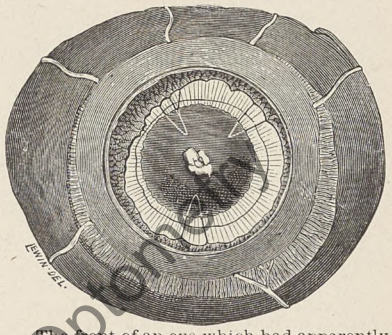
4. One or more fibres attached to the small circle of the iris float free at their other extremities. (Fig. 10.)

Fig. 10.



Section of the fellow-eye to the one shown in Fig. 11, which also had apparently complete absence of the iris. The rudimentary iris is shown with a tag of pupillary membrane proceeding from its free extremity, and a tag of adhesion passing between its root and the back of the cornea. (Trans. Ophth. Soc., vol. xiii.)

Fig. 11.



The front of an eye which had apparently complete congenital absence of the iris; the cornea and sclerotic have been removed and a rudimentary iris exposed. Loops of persistent pupillary membrane pass from the rudimentary iris to the surface of the lens. There is also a congenital anterior polar cataract. (Trans. Ophth. Soc., vol. xiii.)

5. A loop is formed by two fibres in front of the pupil. (Fig. 11.)

6. One or more fibres arising from the iris are attached to the capsule of the lens. This variety is sometimes spoken of as a capsulo-pupillary membrane.

7. A fibre arising from the iris is attached to the posterior surface of the cornea. (Fig. 12.)

This last arrangement is apparently but seldom met with. In some of the cases recorded there has been a history of ophthalmia neonatorum, and an opacity of the cornea was present which rendered it likely that the attachment of the pupillary membrane was the result of inflammation. In the case here figured there was not the least sign of past or present inflam-

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mation, and other congenital abnormalities existed in the eye: so that there seems little doubt that it is a true case of congenital non-separation of the pupillary membrane from the back of the cornea.

The color of persistent fibres of pupillary membrane may be gray, the color of the iris in which they occur, or partially black. This black pigmentation is most frequently seen about the lenticular extremity of a capsulo-pupillary membrane. A portion of the anterior fibro-vascular sheath of the lens or the pupillary membrane may remain persistent on the sur-

FIG. 12.



Congenital adhesion of iris and of a persistent pupillary membrane to the back of the cornea.

face of the lens without having any connection with the iris at all; should it occur at its anterior pole, it will very closely resemble an anterior polar cataract.

Anterior Synechia of Iris and Persistent Pupillary Membrane.—Cases of adhesion of persistent pupillary membrane to the back of the cornea have been recorded by Beck,[1] Samelsohn,[2] Makrocki,[3] and Zinn.[4] In each of the cases related by these authors there seems to have been a possibility that the adhesion was caused through intra-uterine perforation of the cornea. Seeing that the anterior fibro-vascular sheath of the lens, which afterwards becomes the anterior layer of the iris, and the pupillary membrane are developed from the posterior part of the mesoblast which grows in to separate the lens from the cutieular epiblast, the anterior part of which forms the substantia propria of the cornea, it might reasonably be expected that occasionally the anterior fibro-vascular sheath, in part of its extent, would fail to become separated from the cornea, and an anterior synechia of the pupillary membrane or the iris result. The authors of this article have found clinical and pathological evidence that such cases do occur. In the

[1] Ammon's Zeitschrift, Bd. i. Heft. i.
[2] Centralblatt für Augenheilk., 1880, S. 215.
[3] Archiv für Augenheilk., Bd. xiv. S. 83.
[4] Klinische Monatsblatt für Augenheilk., Bd. xxviii. S. 290.

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case which has been described and pictured under polycoria (Fig. 8), in addition to the numerous openings through the iris, a number of little whitish elevations of the iris tissue could be seen coming forward to the back of the cornea. Fig. 12 represents the cornea and iris of an eye in which the central artery of the vitreous was persistent and patent and ended in an opaque membrane behind the lens. The cornea of this eye was quite clear and microscopically appeared perfectly healthy, but adherent to its posterior surface were a large piece of a persistent pupillary membrane and part of the pupillary border of the iris. In Fig. 11, representing the section of the portion of an eye in which the iris appeared clinically to be absent, and in which a rudimentary one was found to be present, a tag of adhesion is seen passing from the anterior surface of the iris to the back of the cornea in the region of the ligamentum pectinatum.

IRIDODONESIS, OR TREMULOUS IRIS.

Cases in which the iris is found to be tremulous from birth are those in which there is ectopia of the lens, or in which the eye is buphthalmic. In both these conditions the posterior supporting structures of the iris are in abnormal relation to it. Occasionally cases are met with in which, on movement of the eye, a slight oscillatory motion of the iris can be detected.

IRIDEREMIA.

Cases are sometimes met with of congenital defect in the eye, in which the iris appears to be entirely absent. On looking at the eye in the part where the iris should be, nothing but blackness, like that of the pupil, is to be seen. Irideremia or aniridia is the term applied to such cases. In others the iris, though to a great extent absent, is seen not to be entirely so, a small crescentic piece or little nodules of iris tissue being found at the periphery of the chamber; these are spoken of as cases of partial or incomplete irideremia. On examination of a case of irideremia with an ophthalmoscopic mirror, a large area of red reflex is obtained, broken, however, at its periphery by a circular dark line, the border of the lens. Outside the margin of the lens a fine striation, due to the fibres of the suspensory ligament, can be made out. In some cases the cornea has an opacity in it, in some the lens is opaque; often there is an anterior polar cataract. In cases of partial irideremia there may be tags of persistent pupillary membrane present. It is always a bilateral affection, the eyes being frequently nystagmic. The sight is defective, and the patient acquires a habit of screwing up his lids, endeavoring to shut off some of the excess of light which enters the eyes. The affection is frequently hereditary.

Microscopical examinations of eyes with irideremia have been made by Pagenstecher[1] and G. Rindfleisch.[2] Fig. 12 represents sections from a case

[1] Klinik für Augenheilk., Bd. ix. p. 425.

[2] Archiv für Ophth., Bd. xxxvii., Abth. 3, S. 192.

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examined by one of the authors (E. T. C.), in which clinically no iris was seen, but in which pathological examination revealed a rudimentary one.

Several theories have been brought forward to account for the absence of the iris in these cases. It was suggested that the iris might have become absorbed together with the pupillary membrane. F. Arnold attributes its absence to failure in the formation of the anterior ciliary arteries. In the case the microscopical sections of which are figured, these arteries were found well developed. The more probable explanation of this defect is that suggested by Manz. He believes the iris to be arrested in its development by an unusually strong union of the lens to the cornea. Rindfleisch attributes this abnormal union or contact of lens and cornea in his case to intra-uterine inflammation of the choroid extending forward and causing perforation near the sclero-corneal margin, with escape of aqueous. It is highly unlikely that an affection which is almost invariably bilateral could be caused in this way. It is, moreover, unnecessary to have a perforation for the lens to come in contact with the cornea, for at the time the iris is developing these structures are in apposition, the anterior fibro-vascular sheath alone intervening.

COLOBOMA OF THE IRIS.

Coloboma of the iris is a deficiency in the tissue of the iris by which the pupil is altered in shape. It is one of the most commonly met with malformations of the eye. The term pseudo-coloboma of the iris is applied to cases in which a portion only of its thickness is wanting in one position, the deeper layers being left exposed.

Coloboma of the iris is nearly always met with in its lower half, and either directly downward, or downward with an inclination inward or outward. Exceptional cases of the defect have, however, been recorded in which it has occurred in other directions. It has been seen directed upward by von Ammon and Theobald;[1] upward and outward by Fage,[2] Theobald,[1] and Frost;[3] upward and inward by Fage[2] and Pollock;[4] outward (Figs. 13 and 14) by Manz, Nuel and Leplat, Makrocki,[6] and Lang;[5] inward by Makrocki.[6] Two colobomata of the iris have been met with in one eye by Manz and Rau.

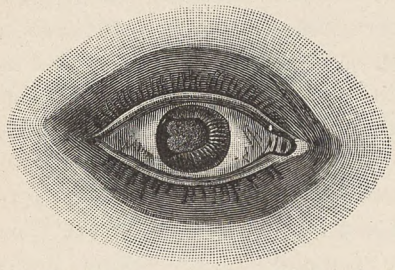
The extent and shape of the defect are even more inconstant than the direction. It may consist only in a slight notching of the pupillary border, or the whole thickness of a sector of the iris may be absent, from the margin of the pupil up to the ciliary body. In some cases the gap left has a sort of shoulder, marking the limit of the original pupil. The edges of the cleft

[1] Trans. Am. Ophth. Soc., vol. v. p. 99.
[2] Gaz. Hebdomadaire des Sciences Médicales de Bordeaux.
[3] Trans. Ophth. Soc., vol. xiii. p. 144.
[4] Archives of Ophth., vol. xii. p. 410.
[5] Trans. Ophth. Soc., vol. x. p. 106.
[6] Archiv für Augenheilk., Bd. xiv. S. 73.

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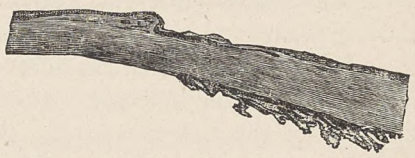
may be parallel to one another; then the gap, together with the normal pupil, will be of the shape of a key-hole. In other cases the edges of the gap converge to a point at the ciliary margin; the gap and the normal pupil then present a pear-shaped opening. A rare form of coloboma is that in which its margins diverge, its base being at the ciliary border. The condition termed coloboma with a bridge is referred to under polycoria. In coloboma of the iris, though a sector of the sphincter muscle is absent, the pupil is

FIG. 13.



Congenital coloboma of iris and lens outward. (Trans. Ophth. Soc., vol. x.)

FIG. 14.



Microscopical appearances in the region of the coloboma of the iris in the eye pictured in Fig. 13. (Trans. Ophth. Soc., vol. xiii.)

found to react to myotics and mydriatics in the usual way. Alone, it gives rise to no defect in vision. The other defects of the eye with which it is often associated are: coloboma of the choroid or ciliary body, coloboma or displacement of the lens, and microphthalmos. (Fig. 15.) Patients affected

FIG. 15.



Microscopical appearance of the front part of a microphthalmic eye with coloboma of the iris. (Royal Lond. Ophth. Hosp. Rep., vol. xii.)

with it are also occasionally found to have other congenital defects, such as harelip, cleft palate, or coloboma of the eyelid.

Coloboma of the iris is not due, as some have supposed, to an unclosed fœtal fissure in that structure. The iris is not developed in two sectors, and the normal fœtal iris never has any cleft; it grows as a prolongation forward from the ciliary body,—not, however, commencing until the two edges of the fœtal fissure in that structure and in the choroid have become united. Should the cleft in the ciliary body remain unclosed, or should the closure be delayed, then either no iris would be formed in the position of the

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cleft, or the time for the development of the iris in that position would be shortened, and it would not attain its normal length.

To this explanation it may be objected that it is difficult to see why the defect should sometimes be situated in the upper part of the iris, the fœtal cleft being below. Pflüger suggested that in these cases some rotation of the eye occurred during fœtal life.

Makrocki supposes the choroidal fissure to be abnormally placed.

Neither of these hypotheses would explain the existence of two colobomata in one eye, or of a horizontal coloboma of the iris with the same defect in the choroid at right angles to it.

It has been suggested that irideremia is due to an abnormal adhesion or late separation of the lens and cornea. Should this adhesion or late separation, instead of involving in the cases of irideremia the whole surface of the lens, involve only a portion of its area, then the iris would be prevented from developing there, but would be formed in the normal way in the rest of its circumference. In this manner a coloboma of the iris might occur in any position, and even two might be formed in the same eye.

CHOROID (CHORIOID).

Congenital abnormalities of the choroid comprise developmental defects in the region of the choroidal fissure, and macula,—*i.e.*, colobomata, defects of pigmentation, and vascular defects.

COLOBOMA OF THE CHOROID.

This defect generally consists in an absence of the choroid along the line of the so-called choroidal fissure. The defective area is usually ovoid, with its long diameter parallel with the antero-posterior axis of the globe; posteriorly it may extend up to, or even beyond, the disk, which is then included in the area; in the latter case there is a coloboma of the sheath of the nerve, and all resemblance to the normal disk surface is lost. Clinically, the anterior extremity of the defect is often invisible; it may be continuous with a coloboma of the ciliary body and iris.

Ophthalmoscopically, the sclerotic, which is left exposed in the region of the coloboma through the absence of the choroid, is of a pearly white color; here and there a little pigment and a few ciliary vessels, which are occasionally crossed by a retinal vessel, are seen on its surface. The floor of the coloboma may be fairly smooth, or in parts depressed, with the bottom of the depression several millimetres below the general level of the surface; when the depressions are very marked they may form cysts. (See Microphthalmos.) The floor may also be raised into little ridges, whilst occasionally it is subdivided by transverse bands of normal choroid. The margins of the area are sharply defined and pigmented.

The retina is frequently absent from the region of the coloboma (Manz),[1]

[1] Graefe and Saemisch's Handbook.

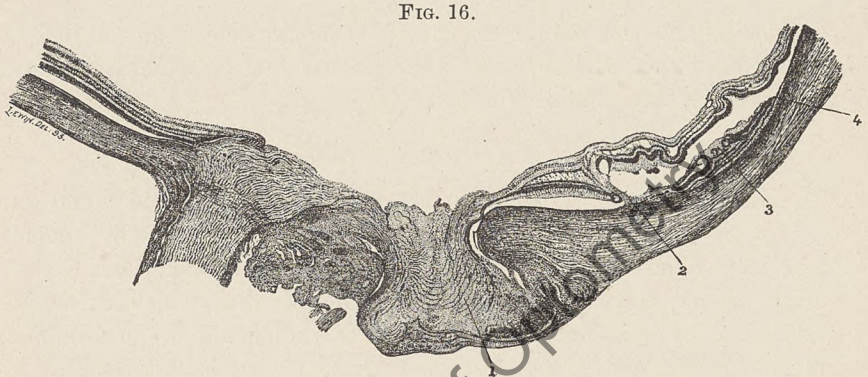
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and when it is present (Pause)[1] the hexagonal epithelium never contains any pigment and the other retinal layers may not be completely differentiated. The occasional presence of the retina accounts for there not being in every case an absolute scotoma corresponding to the coloboma.

Fuchs, in his text-book, states that it is hereditary to a high degree, and attributes the defect in the choroid primarily to the non-union of the edges of the retinal cleft, which does not, however, explain those cases in which the retina exists over the whole area; but they can all be explained if it is considered that the defect is due to an abnormal adhesion of the retina to the mesoblast, so that when this abnormal adhesion takes place before the retinal fissure is closed, the coloboma is devoid of a covering of retina, and an absolute scotoma exists, whereas when it occurs after the closure of the fissure the retina is everywhere present, and there is no scotoma.

The greater frequency of the defect in the region of the retinal fissure is thus explained; but that it is not always situated in this region is shown by the occasional occurrence of similar defects in other parts of the fundus. Thus, Frost[2] records a case of coloboma of the iris and choroid on the tem-

FIG. 16.



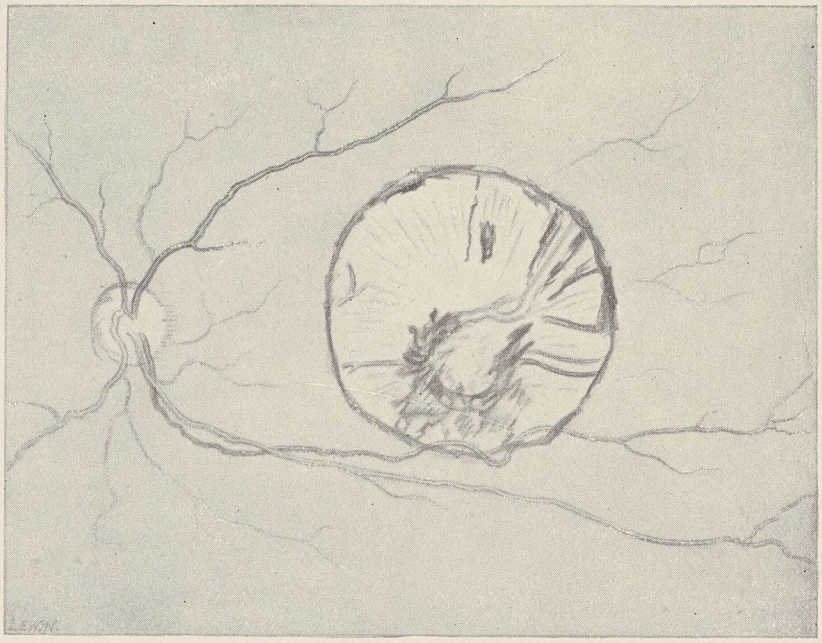
Microscopical appearances of the posterior half of a microphthalmic eye, showing a break in the continuity of the sclerotic through which a mass of nerve-tissue is protruding (1): a coloboma of the choroid commencing at 2; an adhesion between the retina and the uveal pigment-layer replaced for a short distance by tissue simulating retina (3). (Trans. Ophth. Soc., vol. xiii.)

poral side, and other cases are described in which congenital defects of the choroid have been met with in various positions and of widely different shapes (Lang).[3] An isolated patch of non-developed choroid may occur in the same eye with a coloboma of the iris, choroid, and optic-nerve sheath in the region of the fœtal cleft (Wood).[4] The explanation of all the congenital defects of the choroid, wherever situated, is the same: an adhesion forms between the developing retina and the mesoblast, which latter, conse-

[1] Graefe's Archiv, 1878.
[2] Trans. Ophth. Soc., vol. xiii. p. 144.
[3] Ibid., vol. vi. p. 439.
[4] Ibid., vol. xii. p. 173.

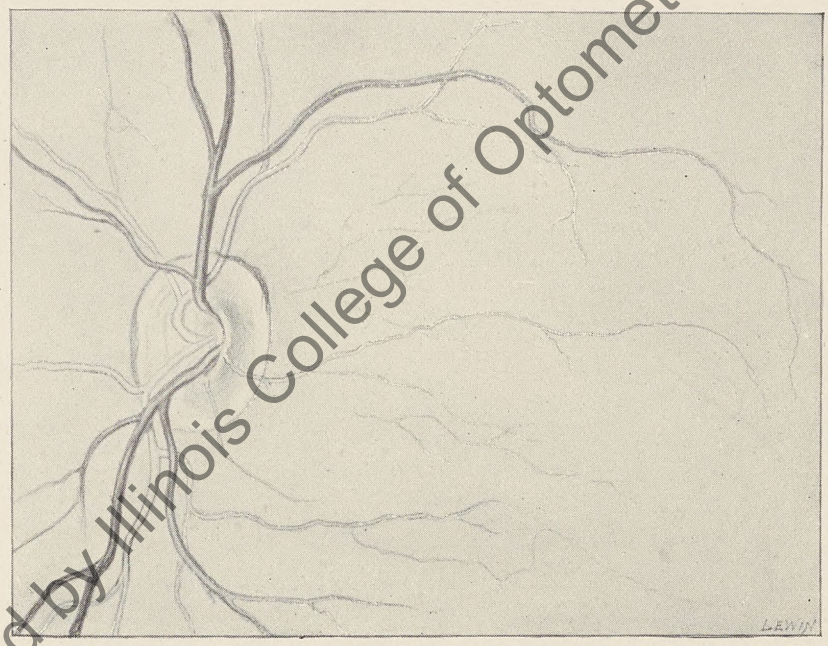
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FIG. 17.



Coloboma of the choroid in the macular region.

FIG. 18.



Unusual appearance of the optic disk, due to the abnormal direction of the head of the optic nerve.

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quently, fails to become differentiated into the choroid and sclerotic; where the choroid is absent, there the pigment fails to be formed in the hexagonal epithelium.

In Fig. 16, between 1 and 2, the retina, the pigment epithelial layer, the choroid, and the sclerotic appear normal, except that the choroid is not pigmented and contains too many cells. Between 2 and 4 the choroid ceases, and the epithelial layer is unpigmented and is adherent to the sclerotic; whilst beyond 4 all the tissues are again normal.

COLOBOMA OF THE MACULA.

This usually consists of a nearly circular defect in the choroid, which exposes a white area of sclerotic, upon which are seen a few scleral vessels and a little pigment. (Fig. 17.) The choroid is deeply pigmented at the margin, where it forms a sharply defined line. The retina passes over the defective area, as may occasionally be recognized by the course of a retinal vessel and by the absence of a scotoma. The depth of the floor may range between one and several millimetres.

FUCHS'S COLOBOMA.

This is a small crescentic defect of the choroid at the lower border of the disk, not unlike a myopic crescent, except in its position; whilst the disk appears as if it were twisted around its antero-posterior axis, so that its long diameter is horizontal and its physiological cup is directed downward.

The retinal vessels usually pass over it in an uninterrupted manner, but occasionally they dip down into a depression which is due to a defect in the optic-nerve sheath or the sclerotic at the same point. The vision of these eyes is usually below normal.

COLOBOMA OF THE SHEATH OF THE OPTIC NERVE.

This may be partial or complete. When partial, it presents the appearance of an extremely deep cup situated at the inner or lower part of the disk. The outline of the disk may be distinguished in part of or in its entire circumference. The retinal vessels, on reaching the margin of the colobomatous area, may dip down and at once be lost to view, or they may dip down and reappear again as they mount on to a slightly higher portion of the disk. In other cases there is a gradual shelving from the margin to the centre of the coloboma, and the vessels do not abruptly disappear.

There may be a coexisting coloboma of the choroid continuous or separated from the coloboma of the nerve-sheath. (Benson.)[1]

Magnus[2] records a case in which it existed with microphthalmos without coloboma of the choroid. In a case of Manz's[3] it was found pathologically

[1] Dublin Journal Med. Soc., 1882.
[2] Klin. Monatsb. für Augenheilk., 1887.
[3] Knapp's Archiv, 1892.

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that the optic nerve-sheath and scleral margin bulged backward into a deep pocket, over which extended normal retina. A condition somewhat similar is seen in Fig. 16.

The defect is attributed to an imperfect closure of the cleft which is originally present in the under surface of the optic nerve.

DEFECTS IN PIGMENTATION.

The pigment of the choroid and retinal epithelium is altogether absent in cases of complete albinism, and the choroidal vessels which give rise to the pink eye (see Iris) are then everywhere visible with the ophthalmoscope.

An angioma of the choroid associated with a nævus of the lids and orbit has been described in pathological specimens by Milles [1] and Lawford,[2] but there is no record of its having been seen with the ophthalmoscope.

RETINA.

Under Congenital Abnormalities of the Retina are comprised colobomata and cysts associated therewith (page 421), opaque nerve-fibres, certain small bright dots, anomalies of pigmentation, and peculiarities in the source and arrangement of the blood-vessels.

OPAQUE NERVE-FIBRES.

The appearance presented by this condition is that of a very bright white area which is usually continuous with the upper or the lower margin of the optic disk, from whence it spreads out and terminates usually in a feathery striated border ; it may be smaller than the disk or many times larger, when it may reach beyond the macular region, or it may completely surround the disk. (Hartridge.)[3]

In some cases a patch is quite separate from the disk, and in others the nerve-fibres show the characteristic appearance in an isolated patch in the retina, but also starting from the disk. The retinal vessels coursing through the patch partly appear on its surface and in part are hidden by the opaque fibres. The condition is due to the retention around some of the axis-cylinders of the medullary sheaths, which normally cease at the lamina cribrosa.

A scotoma in the field of vision corresponds to the opaque area, and in extreme cases of the defect the eye may be amblyopic.

Marcus Gunn [4] describes a change in the retina which can be seen only by the direct method and a low illumination. It consists of a number of small bright "crick-dots," which occur near the disk and anterior to the retinal vessels. They are sometimes hereditary, and may affect several members of a family.

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[1] Trans. Ophth. Soc., vol. iv. p. 168.
[2] Ibid., vol. v. p. 136.
[3] Ibid., vol. v. p. 177.
[4] Ophth. Review, 1889.

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RETINAL VESSELS.

The ordinary vascular supply to the retina by means of the arteria centralis is supplemented in seventeen per cent. (Lang and Barrett)[1] of cases by a larger or smaller branch derived from the posterior ciliary arteries. Nettleship[2] first called attention to the point, and Benson has since shown what a benefit the possession of a double supply confers when the central artery is blocked by an embolus. The cilio-retinal branch may take the place of one of the temporal divisions of the arteria centralis, or of a macular branch. It is characterized by the fact that when it reaches the disk-margin it immediately bends back and disappears, instead of proceeding on to the centre of the disk. It is usually present in one eye only.

The arrangement of the blood-vessels on the disk is very variable. Occasionally they enter the nerve at the margin of the disk, the centre being free from all blood-vessels and very pale in color. (Lawford.)[3] The veins may all unite into one branch, which forms a loop, lying partly on the disk and partly on the retina, before disappearing down the centre of the nerve. (Lawford.)[4] Or a branch of the veins may form a loop and collect other veins (Werner),[5] or two veins may be joined together by a short branch. (Frost.)[6]

Just before reaching the disk, vein and artery may be coiled round each other in a spiral fashion. Again, the artery may form a loop which passes forward from the disk into the vitreous for two or three millimetres and returns again to the disk (Frost); or a vein and an artery may communicate in the retina.

Congenital patches of pigment, in shape and arrangement somewhat like the cells of growing hyaline cartilage, and occurring in a sector-shaped patch in the lower half of the retina, are pictured and described by Stephenson.[7] They produce no symptoms, and are discovered only on a systematic examination of the eye. Stephenson suggests that they are due to extension of the pigment from the outer into the inner layers of the retina. Minute round dots of pigment, which appear to be the size of a pin's point by the indirect method of ophthalmoscopic examination, are of more frequent occurrence. For Albinism, see page 435.

Retinitis pigmentosa and glioma of the retina, which occur at times as congenital defects, do not differ from the same conditions seen at a later period.

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[1] Royal Lond. Ophth. Hosp. Rep., vol. xii. p. 59.
[2] Ibid., vol. viii.
[3] Trans. Ophth. Soc., vol. xv.
[4] Ibid.
[5] Ibid., vol. x.
[6] Ibid., vol. xi.
[7] Ibid., vol. xi. p. 77.

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OPTIC NERVE.

Apart from the coloboma of its sheath, which is described at page 445, the congenital defects of the optic nerve consist of alterations in the direction of the nerve-head, so that it appears to be reversed, and what is ordinarily the outer or temporal pale part of the disk is turned towards the nose (see Fig. 18), of pigment particles occurring in the superficial part of the disk, and of absence of the central retinal vessels, of which a case has been recorded by Berry.

Congenital atrophy of the disk does not ophthalmoscopically differ from post-natal atrophy, neither does the congenital glaucoma cupping differ from that condition when produced after birth. (See Buphthalmos.) The appearances produced by remains of the hyaloid artery on the disk are described under Abnormalities of the Vitreous.

CONGENITAL ABNORMALITIES OF THE LENS.

The lens may be congenitally absent (aphakia). It may be altered in size, in shape, in position, and in transparency.

APHAKIA.

In many cases in which the lens is apparently absent, it is really only displaced out of sight. In fact, it is very doubtful whether a seeing eye could be produced if the downgrowth of cuticular epiblast which results in the formation of the lens failed to occur. Cases where the lens appeared totally absent have been observed in microphthalmic eyes by Seiler, von Ammon, and Hermann Becker.[1] In the case reported by Becker the following conditions were also found: absence of pupil, iris, ciliary body, and anterior chamber, coloboma of retinal pigment epithelium and choroid, and thinning of sclerotic.

CONGENITAL SMALLNESS OF THE LENS.

An unusual smallness of the lens is detected only on examination of the eye with the ophthalmoscope after the pupil has been dilated with atropine. The edge of the lens is then seen as a dark ring standing out against the red reflex of the fundus, and an unusually large space is found between it and the margin of the dilated pupil. The anterior chamber in such cases is usually deeper than normal, and the iris is tremulous.

In a case recorded by Hartridge[2] the patient was highly myopic.

LENTICONUS.

Lenticonus is the term applied when the lens presents an abnormal curvature of either its anterior or its posterior surface,—a condition of things

[1] Archiv für Ophth., Bd. xxxiv., Abth. 3, S. 103.
[2] Trans. Ophth. Soc., vol. vi. p. 489.

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that is very similar to keratoconus. Conicity of the surface of the lens is a rare form of abnormality; it seems to be more frequently met with in connection with its posterior than with its anterior surface, for there are only two cases recorded in which the latter was affected, while there are twelve of the former. The two cases of anterior lenticonus are described by Webster and Placido; in both it was bilateral, and in both there was some doubt as to whether it was congenital or acquired. It is a condition which can be easily detected by focal illumination.

Posterior lenticonus may be diagnosed by seeing, on illumination of the fundus with the ophthalmoscopic mirror, a sharply outlined disk in the centre of the illuminated area, having the appearance of an oil-drop in the lens. The fundus is visible through the central disk, but it is found, either by estimation with the direct method or by retinoscopy, that there is a difference in the refraction of the central disk and of the sides of the lens. The condition is sometimes associated with opacities in the lens at the posterior pole or elsewhere. In Meyer's case a remnant of the hyaloid artery was adherent to it; in other cases the lens was quite clear. These latter cases L. Müller[1] believes not to be due to conicity of the lens, though he asserts that the former are. He explains the appearances seen by supposing that there is some undue thickness or thinness of the nucleus. He would prefer to describe them as cases of lenses with a double focus.

COLOBOMA OF THE LENS.

This is a rare form of malformation, and consists of a defect in the margin of the lens, nearly always the lower. Two exceptional cases are on record: one by Schiess,[2] where it was situated at the lower and outer border, and the other by Lang,[3] in which it was directly outward. (Fig. 13.) The defect consists in a triangular or saddle-shaped notch extending through the whole thickness of the lens, and varying in amount from a slight indentation to as much as one-fourth of its substance; or in the lower margin of the lens presenting instead of its normal curvature a straight or a crenated line.

A remarkable case has been described by Doyne,[4] in which there was a coloboma of the iris and choroid, and the corresponding margin of the lens, instead of being notched, presented a projection.

The malformation may occur in one eye only or in both, and is frequently associated with other abnormalities, such as coloboma of the iris, ciliary body, or choroid. A defect in the suspensory ligament corresponding to the notch in the lens is occasionally seen. The lenses thus affected may also be congenitally displaced, smaller than normal, or partially opaque.

The refraction of eyes with coloboma lentis is usually myopic. In patients who have had the defect in one eye only, it has been found that the

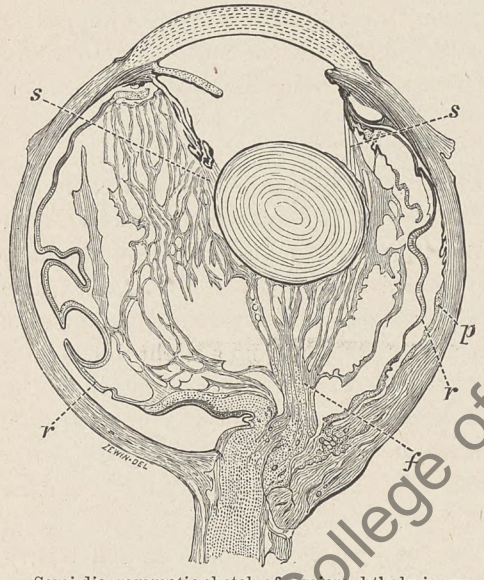
[1] Klinische Monatsbl. für Augenheilk., 1894, S. 178.
[2] Ibid., 1871, S. 99.
[3] Trans. Ophth. Soc., vol. x. p. 106.
[4] Ibid., vol. xi. p. 220.

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defective eye is myopic, the other being emmetropic. Two cases have been recorded by Bowman[1] and Heyl[2] in which there was hypermetropia. The abnormality is caused by some defect in the development of the suspensory ligament. As has been already mentioned, this is developed by adhesions forming between the sides of the lens and the ciliary body at that period of fœtal life when they lie in contact. Should some of these adhesions fail to occur, then, as the eyeball enlarged, that portion of the capsule to which no suspensory ligament was attached would not be held taut and made to expand like the remainder; consequently there would be a depression in the lens at that situation. The amount and shape of the deficiency would depend on the extent of the defect in the suspensory ligament. The most likely cause for the absence of adhesions between the ciliary body and the side of the lens, with a consequent defect in the suspensory ligament, would be an absence of the ciliary body; and, as we have already said, a coloboma of the ciliary body is frequently found associated with coloboma of the lens.

ECTOPIA OF THE LENS.

FIG. 19.



Semi-diagrammatic sketch of a microphthalmic eye. —*f*, fibrous tissue in centre of vitreous holding lens back; *s*, suspensory ligament of lens stretched and attached to elongated ciliary processes; *r*, retina much folded; *p*, position at which the choroid in the lower part of the eye commenced, and where the pigmented epithelial layer first became pigmented. (Trans. Ophth. Soc., vol. xiii.)

Congenital displacement of the lens is usually bilateral, but may be present in one eye only. It is not a malformation which is commonly met with: out of fifty thousand hospital and private patients of Knapp's, only $\frac{1}{5000}$, or ten, of these cases were seen. It is sometimes met with in several members of one family. Morton[3] has recorded how, presumably, it occurred in five successive generations, comprising seven individuals. The direction in which the lens is displaced varies; in the large majority it is upward, either directly or with a slight inclination inward or outward. It has been seen displaced horizontally, also downward and outward, or downward and inward, but not directly downward. (Fig. 19.) Displacement backward occasionally occurs in microph-

[1] Royal Lond. Ophth. Hosp. Rep., vol. v. p. 12.
[2] Rep. of Fifth Internat. Ophth. Cong., 1876, p. 16.
[3] Royal Lond. Ophth. Hosp. Rep., vol. ix. p. 435.

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thalmic eyes : this is due to some defect in the development of the vitreous, and will be further dealt with in connection with abnormalities of that structure.

The direction in which the lenses are displaced is usually symmetrical in the two eyes, but not always so ; for example, the authors have recently had under their observation a boy in whom the right lens was displaced directly upward and the left directly outward. Monocular diplopia is not a common complication : Knapp met with a case in which four images were perceived simultaneously with the two eyes.

On examination of eyes with congenitally displaced lenses, the iris will be found tremulous, the anterior chamber deep and often of uneven depth in different parts, it being deepest in the part from which the lens is displaced. On oblique illumination the margin of the lens will be seen as a curved line, the lens itself gray, and the aphakic part at its margin black. Sometimes the displacement is so slight that the margin of the lens cannot be detected until the pupil has been dilated with atropine. With the ophthalmoscopic mirror the curved edge of the lens is seen as a dark line ; it is not always quite regular, sometimes having slight depressions or elevations on it. In a case of Marcus Gunn's [1] there was a deep notch in its margin, constituting a coloboma.

Displaced lenses are often smaller than normal, and altered in shape, being rounder than they should be, thus resembling the fœtal lens. They are usually quite clear, but may have opacities in them. The condition of the suspensory ligament between the margin of the lens and the ciliary body from which it is displaced varies ; sometimes it is absent in this position ; at other times a few fibres are visible here and there ; in other cases, again, except for the stretching, it appears normal. When the suspensory ligament is absent the lens is mobile. A case of this sort is recorded by Sir W. Bowman,[2] in which, apparently, the lens at times swayed forward, blocked the passage of fluids through the pupil, and so caused increase of tension. The most common malformations of the eye with which ectopia lentis is complicated are corectopia, coloboma, irideremia, and nystagmus.

Congenital displacement of the lens, like coloboma of the lens, is due to some defect in the development of the suspensory ligament. In the former the defect is more extensive than in the latter, and is probably occasioned by a failure or late closure of the ocular cleft in the ciliary region, so that as the eye expands there is no suspensory ligament to hold the lens down in that region, and it consequently becomes drawn in the opposite direction. The most common position in which lenses are displaced, as has been already mentioned, is upward, either directly or with a slight inclination inward or outward,—that is, opposite to that in which the fœtal ocular cleft is usually met with. Displacements might also be occasioned

[1] Trans. Ophth. Soc., vol. ix. p. 166.
[2] Royal Lond. Ophth. Hosp. Rep., vol. v. p. 1.

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by the adhesions between the ciliary body and the margin of the lens being denser on one side and less elastic than normal, so that they expand less readily than those on the opposite side; this would account for those cases in which fibres of the suspensory ligament can be seen stretching across the aphakic area.

CONGENITAL CATARACTS.

Congenital cataracts may be divided into those in which the opacity extends throughout the lens and those in which only a portion of the lens is opaque. The partial cataracts may be further subdivided into (1) anterior polar cataracts, (2) posterior polar cataracts, (3) lamellar cataracts, (4) nuclear cataracts, (5) dotted cataracts.

1. *Anterior Polar Cataracts.*—The term anterior polar or pyramidal cataract should be confined to those cases in which an opacity is situated at the anterior pole of the lens, within the capsule,—that is, opacities of the lens itself. It should not be applied to those in which the opacity is external to the capsule and due to a persistence of a portion of the pupillary membrane. Clinically, it is often very difficult to localize exactly the position of the opacity, and sometimes, possibly, the two forms are associated. That a true anterior polar cataract without any opacity external to the capsule may be congenital is proved by a case of one of the authors (E. T. C.), in which the eyeball was obtained for pathological examination. In it the lens-capsule at the anterior pole was raised and wrinkled, it having immediately beneath it a mass of laminated hyaline substance and scattered epithelial cells. This mass presented microscopical appearances precisely similar to those seen in pyramidal cataracts which occur after ulceration of the cornea.

2. *Posterior Polar Cataracts.*—This form of cataract is sometimes said to be congenital. It is possible, however, that the cases so recorded have been ones in which portions of the posterior fibro-vascular sheath of the lens have remained persistent and attached to the external surfaces of the capsule; therefore not really opacities of the lens itself.

3 and 4. *Zonular and Nuclear Cataracts.*—Zonular or lamellar cataract is the name given to that form of opacity of the lens in which there is a layer of opaque substance situated between a clear nucleus and a clear cortex. It is distinguished from nuclear cataract by illumination of the eye with the ophthalmoscopic mirror, when the margin of the disk is seen to be darker than the centre; whereas when the nucleus is opaque the centre of the disk is as dark as or darker than the edge. In some rare cases a second complete or partial layer of opacity is present, the two being separated by clear substance. Frequently on the surface of the disk of opacity streaks or dots of denser opacity are seen, which may project beyond it into the clear cortex, when they produce much the appearance of the handles of the steering-wheel of a ship. There has been much discussion as to whether lamellar cataract is congenital, or whether it occurs during the first few years of infancy. Measurements of the zone of opacity and

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measurements of the fœtal lens show that the former is never larger than the lens at birth, that it may be about the size of it at that time, and that it is usually smaller, sometimes very much smaller. From this it must be concluded that lamellar cataract is produced before birth, or that the part affected at the time the change occurs is not the most peripheral, as has generally been supposed. Certainly lamellar cataract occasionally comes on after birth, for Graefe has recorded a case in which the opacity was caused by iritis and synechia, Beselin and Schirmer recorded cases following ulceration of the cornea, and one of the writers of this article has seen a case in which the opacity was brought about in the same way.

Von Graefe[1] and Jäger[2] were the first to bring forward anatomical proof of the lamellar character of this form of opacity; they found, on section of lenses presenting the appearances described, which had been extracted, that there was an opaque whitish line separating a clear nucleus from a clear cortex. During the last few years much has been written on the microscopical appearances of lamellar cataract by Deutschmann,[3] Beselin,[4] Schirmer,[5] Lawford,[6] Hess, and Treacher Collins.[7] The outcome of these observations seems to be that there are three sorts of changes met with. First, fissures between the lens-fibres which may or may not contain a granular substance, and which run concentric to the nucleus, separating it from the cortex. Second, small vacuoles, the average size of which is .005 millimetre across; they are mostly round or oval, but in places where they seem to have run into one another they are elongated and beaded. Some of them contain a hyaline substance, which after prolonged immersion in logwood stains deeper than the surrounding lens-fibres. Third, spaces larger than the so-called vacuoles, measuring on an average .02 millimetre across, mostly circular, with very irregular margins, and containing a granular substance which stains deeply with logwood. Apparently some degeneration of lens-substance has occurred in their formation. These three changes correspond to the appearances seen clinically in these cataracts,—viz., radiating spokes, the uniform haze, and dots.

5. *Dotted Cataracts.*—Numerous small, scattered congenital opacities are sometimes seen in the lens, in the form either of circular patches or of little streaks. They are most frequently situated in the peripheral parts, and do not give rise to any defect in the acuity of vision. The condition is generally hereditary.

Complete Congenital Cataracts.—Complete congenital cataracts may be divided into three classes, according to their consistency:

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[1] Archiv für Ophth., Bd. i. S. 236.
[2] Staar und Staar-Operationen, 1854, S. 17.
[3] Archiv für Ophth., Bd. xxxii., Abth. 2, S. 295.
[4] Archiv für Augenheilk., Bd. xviii. S. 71.
[5] Archiv für Ophth., Bd. xxxv., Abth. 1, S. 147.
[6] Royal Lond. Ophth. Hosp. Rep., vol. xii. p. 184.
[7] Lancet, December, 1894.

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1. Those in which it is quite fluid, the capsule being simply a bag containing the opaque, liquid, degenerate lens-substance, which, when the former is punctured, runs out and can be at once evacuated.

2. Cases in which the lens presents a milky-white, uniform opacity, but in which it retains much of the normal gelatinous consistency of a juvenile lens.

3. Cases in which the opacity is densely white, and where the lens is apparently shrunken and flattened; in these the pupil will often not respond well to a mydriatic. A very probable explanation of such cases is that the opacity and failure in development of the lens are secondary to a persistence and thickening of the posterior fibro-vascular sheath, together with persistence of the central artery of the vitreous. The opaque membrane remaining after discission is the thickened fibro-vascular sheath or abnormally developed vitreous, which, being composed of fibrous tissue, would not be acted upon by the aqueous humor. (See Abnormalities of the Vitreous.)

CONGENITAL ABNORMALITIES OF THE VITREOUS.

The congenital abnormalities of the vitreous humor which are met with proceed from the persistence of some portion of the vascular system which exists in it during fœtal life, or from what has been aptly termed by Hess atypical embryonic development of the mesoblastic tissue from which it is derived. The blood-vessel which in fœtal life courses through the vitreous is continuous, as has been already stated, with the central artery of the optic nerve. It lies in a canal bounded by a hyaline membrane, and for a portion of its extent is surrounded by a cellular sheath; it is generally continued as a single vessel to the posterior surface of the lens, where it breaks up into branches which supply the posterior vascular sheath of that structure. In some eyes, however, it branches dichotomously several times in its course through the vitreous.

It is important to bear these several points in mind, because so many different anomalies are produced by persistence of one or more portions of this system. These various anomalies may be classed as follows:

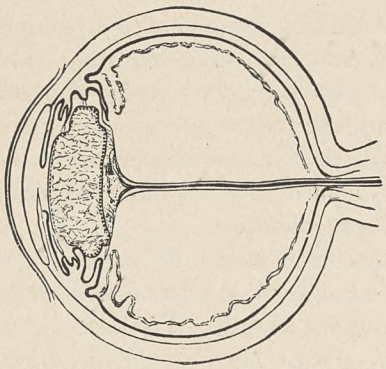
1. That in which the whole artery, with the cellular sheath around the posterior part of it, remains as in the fœtal eye, and continues to carry blood. (Figs. 20 and 21.) A few such cases have been seen with the ophthalmoscope, the presence of blood in the artery having been diagnosed by the red color which it presented. In some of these certainly, and probably in all, a portion of the posterior fibro-vascular sheath of the lens also existed, the vessels of which, by retaining their connections with those of the ciliary body, allowed of the exit of the blood traversing the abnormal artery. In several eyes in which a persistent and patent hyaloid artery was found on dissection, it ended in a mass of fibrous tissue at the back of the lens. (Vassaux, Haab, Hess, Treacher Collins.)

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These cases will be referred to again in considering atypical development of the Vitreous.

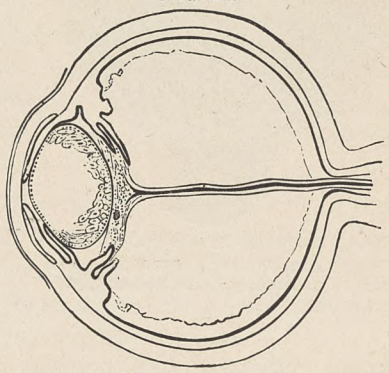
2. That in which the artery persists as a band through its whole length, but does not carry blood. In such cases the band can be seen with the ophthalmoscope stretching from the optic disk to the posterior pole of the lens, to both of which it is adherent. It is frequently noticed to oscillate on movement of the globe, and is generally larger at its two extremities than in the centre. In a few cases the band coming from the

FIG. 20.



Diagrammatic representation of the section of an eye with a persistent and patent hyaloid artery which terminated in a thick fibrous membrane at the back of the lens. (Royal Lond. Ophth. Hosp. Rep.. vol. xiii.)

FIG. 21.



Diagrammatic representation of a case very similar to that depicted in Fig. 20.

optic disk has been observed to divide several times in the vitreous before reaching the back of the lens. When an undivided band is present, its point of attachment to the lens is not always central, but is frequently a little to one side or the other; sometimes there is a stellate opacity of greater or less density in which it terminates.

3. That in which there is a remnant of the artery attached to the optic disk which ends in a free extremity in the vitreous, and in which there is also an opacity at the back of the lens. The remnant attached to the disk is often a long, thin cord which is seen by the ophthalmoscope to lash about in an undulating way on movement of the eye.

An interesting case of the second class is recorded by Unterhamscheit[1] in a myopic lad aged fourteen, which three years later was found to have become converted into one of the third class, the band having given way on account of the elongation of the eye from increase of the myopia.

4. That in which the lenticular end of the artery has alone remained, its hindermost end being free and mobile in the vitreous. It is a variety which is rarely met with. De Beck[2] could find only eight recorded cases of it.

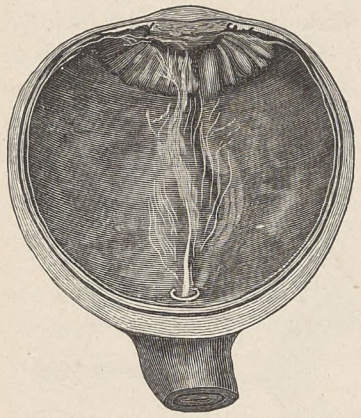
[1] Klinische Monatsb. für Augenheilk., Bd. xx. S. 240.

[2] Persistent Remains of the Fœtal Hyaloid Artery, Cincinnati, 1890.

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5. That in which the neural end of the artery remains, the lenticular extremity having completely disappeared. (Fig. 22.) This is the commonest variety of any. A thin, narrow cord is seen with the ophthalmoscope attached by one end to the optic disk, the other ending free in the vitreous. Its length varies considerably in different cases. It may be of a dark color and quite easily seen, or of a light gray and semi-transparent tint, so that it is readily overlooked. The free extremity of the cord is sometimes rounded and knob-like, at other times fine and tapering; occasionally the band may bifurcate once or oftener. It generally oscillates with an undulating motion on movement of the eye, but occasionally is fixed and immobile.

FIG. 22.



Shrunken globe in which a tag of a persistent hyaloid artery was found adherent to the optic nerve on pathological examination.

6. As stated above, the posterior part of the central hyaloid artery is surrounded by a cellular sheath. The artery may become obliterated, but portions of this sheath may remain as fibrous membranes or shreds of tissue attached to the optic disk, filling up the depression normally left in the nerve-head by the divergence of the nerve-fibres. Such gray membranes or tags of tissue are quite commonly seen ophthalmoscopically in otherwise perfectly normal eyes, and one of the authors has examined two of them microscopically, and found them composed of cells and fibres similar to those forming the sheath of the artery in the fœtal state.

7. Little rounded bodies of a steel-gray color, which appear to be fluid-containing cysts attached to the optic disk, are occasionally met with as a congenital abnormality, and must be in some way connected with the fœtal vascular apparatus for the vitreous. It is not evident whether they are cystic distentions of the persistent sheath of the artery or cystic distentions of the artery itself.

8. Some observers have seen appearances in the vitreous which they have thought pointed to persistence of the hyaline canal in which the artery lies, it and its cellular sheath having disappeared. It is usually believed that part of this canal exists in the normal eye (the canal of Stilling), but that it is not visible with the ophthalmoscope. Alteration, either in its contents or in its extent, may possibly in some cases render it so.

9. Congenital opacities at the posterior pole of the lens are probably many of them due to persistence of portions of the fibro-vascular sheath of the lens, the vessels of which are derived in the fœtal state from the division of the central hyaloid artery.

Several cases have now been recorded in which the vitreous humor has

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been found in a part of its extent to have been replaced by a mass of fibres and cells, and this in eyes in which the other structures showed not the least sign of active or past inflammation. This fibrous and cellular tissue has been found located in different positions, sometimes forming a thick membrane behind the lens (Figs. 20 and 21), in other eyes a mass in the region of the ocular cleft or a thick band passing through the centre of the globe from before backward. (Fig. 19.) The eyes in which it was found were many of them microphthalmic, and the central artery of the vitreous was also usually persistent and patent.

When the abnormal tissue is situated as a membrane behind the lens, if that structure has remained clear, a yellowish-gray reflex is obtained from immediately posterior to it, and the appearances of glioma of the retina are closely simulated, which has several times led to a mistaken diagnosis and excision of the globe. When it has formed a band passing through the vitreous, it has sometimes held the lens back while the globe has increased in size, and so brought about a congenital displacement of the lens. Hess explains the presence of this fibrous and cellular tissue by supposing that the mesoblastic tissue which grows inward to form the vitreous, instead of expanding into that structure in the normal way, has undergone what he terms an atypical form of development.

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THE DIOPTRICS OF THE EYE.

BY EDWARD JACKSON, A.M., M.D.,

Professor of Diseases of the Eye in the Philadelphia Polyclinic; Special Lecturer on Physiological Optics in the University of Colorado, Denver, Colorado, U.S.A.

LIGHT, according to the undulatory theory, which best correlates its phenomena, consists of series of vibrations of the extremely tenuous and elastic ether which pervades space, interpenetrating all substances, and being present in a so-called vacuum. These vibrations travel with extreme rapidity (186,380 miles per second in vacuum), and are very minute. The following table gives the number of complete vibrations or wave-spaces for light of different colors contained in a single millimetre of space. The letters indicate the Fraunhofer lines, giving the exact position of the light in the solar spectrum.

Color of Light.	Fraunhofer Line.	Waves per Millimetre.
Red	B	1305
Orange	C	1524
Yellow	D	1697
Green	E	1898
Blue	F	2058
Indigo	G	2331
Violet	H	2540

Substances which permit the passage through them of the luminous vibrations of ether are said to be *transparent*. Those that do not permit the passage of such vibrations are opaque. Any transparent substance may be a *dioptric medium*. When the surface of such a medium is smooth, light can pass freely through it, and it constitutes a *dioptric surface*. When the surface of a dioptric medium is such that it turns the vibrations that were about to pass from it back into the medium, it is a *reflecting surface*.

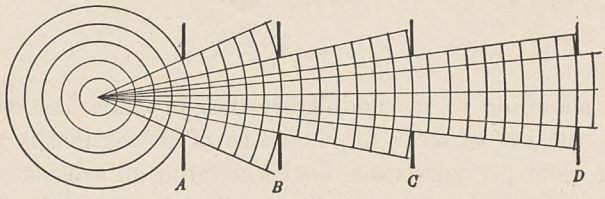
Waves of light, like all other waves, move with always the same velocity in the same medium, and move in a direction perpendicular to the wave-crest or wave-front. The line along which are moving the corresponding points of the successive waves is called a *ray of light*. A number of adjoining rays constitute a *pencil of rays*, the path of an appreciable portion of successive waves. Rays falling on a dioptric or reflecting surface are called *incident rays*.

From each luminous point light passes off equally in all directions,

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unless interrupted by some opaque substance; and, each part of it travelling with equal rapidity from the point of origin, a wave-front constitutes the surface of an enlarging sphere, of which the rays of light are radii. Taking a limited pencil of rays, a limited part of the wave-fronts, the farther we go from the point of origin the flatter the wave-fronts become; and the less divergent the more nearly parallel are the included rays. This is illustrated by comparing the wave-fronts of light, and the rays represented as passing the equal openings at *A*, *B*, *C*, and *D*, in Fig. 1. In ophthal-

FIG. 1.



mology we have to consider the pencil of rays entering the pupil. When this comes from a distance of twenty feet or more, it is customary, although not strictly accurate, to speak of the rays as parallel.

CATOPTRICS, OR THE REFLECTION OF LIGHT.

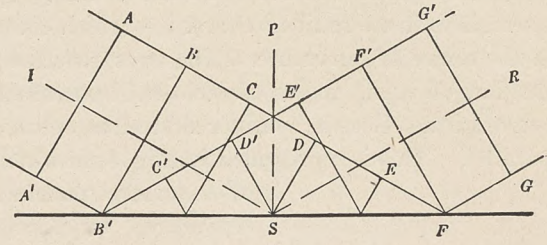
All dioptric surfaces are also reflecting surfaces, the proportion of light transmitted through them and the proportion reflected from them varying with the substances which they separate and the angle at which the vibrations strike. Other than dioptric surfaces are also reflecting surfaces, as the polished surfaces of opaque bodies and all irregular surfaces. From a polished surface light is reflected in a definite direction, the vibrations preserving their original characters: this is called *regular reflection*. This kind of reflection enables one to see the object from which the light came to the surface. But from irregular surfaces (and from polished surfaces in so far as their polish is imperfect) light is reflected in all directions, often with considerable alteration of the vibrations. This is *irregular reflection*. It enables us to see the reflecting surface. All bodies that do not of themselves emit light are thus rendered visible. For instance, of the light thrown into the eye with the ophthalmoscope, the bulk is irregularly reflected from the retina and choroid, enabling the surgeon to see these membranes; but a part is regularly reflected from the smooth surface of the cornea and a part from the smooth surface of the retina, giving the annoying corneal reflex and the instructive retinal reflexes, both of them more or less imperfect images of the source of light. We are here chiefly concerned with regular reflection.

In *regular reflection* the wave-fronts have, after reflection, an inclination to the reflecting surface opposite in direction but equal in amount to their

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inclination to that surface before striking it. This is illustrated in Fig. 2, in which AA', BB', CC', DD', EE', FF', and GG' represent successive wave-fronts, or successive positions of the same wave-front, coming from the direction of I, and reflected by the surface S in the direction R. IS represents an incident ray, and SR a reflected ray. PS is the perpendicular to the reflecting surface at the point S. IS and SR necessarily lie in the same plane perpendicular to the reflecting surface. The angle which the incident wave-fronts make with the reflecting surface, or its equal, the angle ISP, which the incident ray makes with the perpendicular to that surface, is called the *angle of incidence*. The angle which the reflected wave-front makes with the reflecting surface, or the angle PSR which the reflected ray makes with the perpendicular, is called the *angle of reflection*. *The angle of incidence always equals the angle of reflection.*

Fig. 2.



Reflection by a Plane Mirror.—The perpendiculars or normals to a plane surface, PS, $P'S'$, and $P''S''$, Figs. 3 and 4, are all parallel. Hence when parallel rays fall on a plane reflecting surface, each forms with the normal at its point of incidence the same angle of incidence, and, consequently, the same angle of reflection; and they all pass off, after reflection, still parallel. Thus, in Fig. 3, the rays coming from I and reflected from S' pass off towards

Fig. 3.

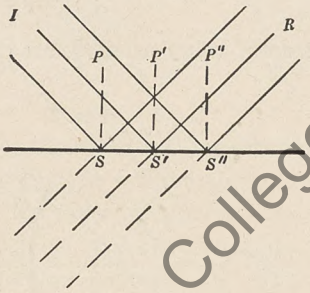
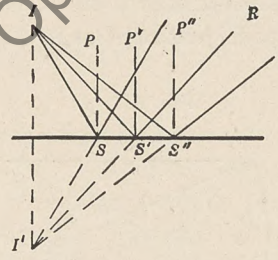


Fig. 4.



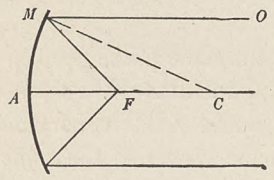
R, still parallel. Again, if the incident rays be divergent, they will continue after reflection equally divergent. Thus, in Fig. 4, rays divergent from I are reflected to R, as though they were diverging from I' situated in the same perpendicular to the mirror as I, and equally distant from it on the opposite side. If the incident rays are convergent, they continue so after reflection. Thus, if in Fig. 4 the incident rays are supposed to come from R, converging towards I', they will, after reflection, continue to

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converge to *I*. *Reflection by a plane mirror does not alter the parallelism, divergence, or convergence of rays.*

Reflection by a Concave Spherical Mirror.—When the reflecting surface is spherical and concave, like the ordinary ophthalmoscopic mirror, the normals to it are radii of curvature, which converge and meet in front of it at the centre of curvature. The rays reflected from such a surface, under the law of equal angles of incidence and reflection, are rendered relatively convergent. Let us consider first what occurs when the incident rays are parallel. This is represented in Fig. 5, in which *AM* represents the section of a concave spherical mirror and *C* its centre of curvature. Of a pencil of parallel rays falling on the mirror, the one passing through *C* and incident at *A* is perpendicular to the reflecting surface and is reflected back upon itself. Another ray, *OM*, incident at *M*, makes with the normal (the radius) *CM* an angle of incidence *OMC*, and is reflected towards *F*, making an angle of reflection *CMF* equal to *OMC*. In the triangle *CMF* the angle *FCM* is also equal to *OMC*, because *OM* is parallel to *CA* and *CM* common to the two angles. Hence *FCM* and *FMC* are equal, and therefore *FM* equals *FC*. When *AM* is a comparatively small arc, *AF* is very nearly equal to *FM* or *FC*, and *F* may be regarded as midway between *A* and *C*. All rays parallel to *AC* and sufficiently near the central ray will thus be reflected to *F*, which is called the *principal focus* of the mirror. Its distance *AF* from the mirror is the *principal focal distance*, and is half the radius of curvature. For rays farther removed from the central ray, and therefore striking the reflecting surface more obliquely, *AF* becomes decidedly shorter than *FC*, so that rays are perfectly focussed by a concave mirror only when they fall nearly perpendicular to its surface.

Fig. 5.



If the incident rays, as in Fig. 6, instead of being parallel, are divergent

Fig. 6.

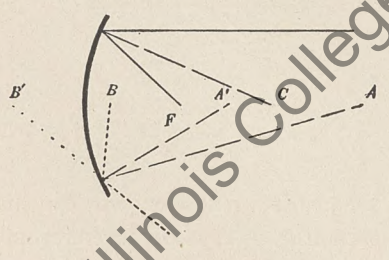
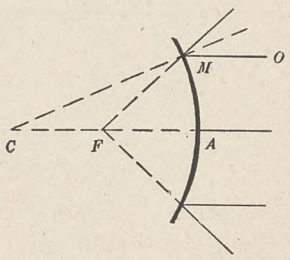


Fig. 7.



from any point beyond *C*, as *A*, the angles of incidence and reflection are smaller, and the focus falls farther from the mirror and nearer the centre of curvature at *A'*. If the rays diverge from the centre of curvature *C*, they fall perpendicularly upon the mirror and are reflected back to that point.

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From points between C and F they will be reflected to points beyond C, as from A' to A. From F the mirror renders them parallel; and from points between F and the mirror, as B, they remain divergent after reflection, as though from a point B' back of the mirror, called a *virtual focus*. When rays from one point are reflected to a focus at a second point, rays from the second are reflected to a focus at the first. Such points are, therefore, said to be *conjugate foci*. The point within the focal distance from which rays diverge, and the point back of the mirror from which, after reflection, they appear to diverge, as B and B', have the same relation.

Reflection by a Convex Spherical Mirror.—This, as it occurs from the surface of the cornea, is the subject of study by the ophthalmometer. It is illustrated in Fig. 7, in which the lettering corresponds to that of Fig. 5. The ray perpendicular to the surface is reflected upon itself, and the ray OM is caused to diverge, as from F, the *principal* (virtual) *focus* of the convex mirror. Rays divergent when they strike such a mirror are rendered more divergent by it. Only rays more convergent before reflection than the normals to the points on which they fall remain after reflection convergent to an actual focus in front of the mirror.

Formation of Images by Mirrors.—For the *plane mirror* this is illustrated in Fig. 8. In general, corresponding points of an object and its

FIG. 8.

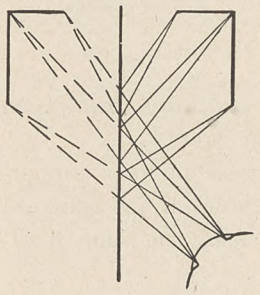


FIG. 9.

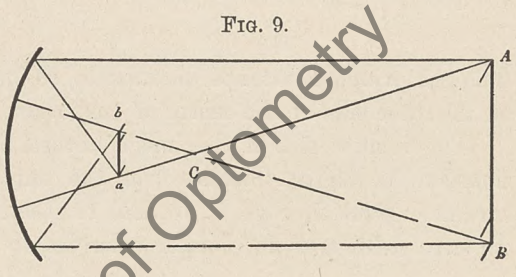


image are symmetrical as regards the reflecting surface, and equally distant from that surface. This causes a sort of lateral reversal of the image as compared with the object, but not any reversal in the direction parallel to the mirror. A familiar example of this is the "reversal" of print or manuscript seen in a mirror. The symmetry of corresponding points also causes the image exactly to equal the object in size.

With the *concave mirror* the image of each point of an object is formed on the ray that passes from that point through the centre of curvature of the mirror. This leads to a complete reversal of the image as compared with the object when these are on opposite sides of this centre of curvature, but only a partial or lateral reversal like that of the plane mirror when both are on the same side of this centre of curvature.

In Fig. 9 the object AB is situated beyond the centre of curvature.

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Hence the image *ab* is situated between the centre of curvature and the principal focus. When the object is situated between the centre of curvature and the principal focus, as at *ab*, the image is in front of the mirror and beyond the centre of curvature, as at *AB*. When the object is situated between the principal focus and the mirror, its image is virtual and situated behind the mirror, as shown in Fig. 10, and the farther the object from the mirror (the less divergent the rays) the farther will the image be from it.

With a *convex spherical mirror*, the object being always in front of the mirror and the rays divergent, the image will always be back of the mirror (see Fig. 11); and since the nearer the object to the mirror the more divergent the incident rays, the more divergent will the reflected rays be also, and the closer the image to the mirror. In general, the image is closer to the mirror

FIG. 10.

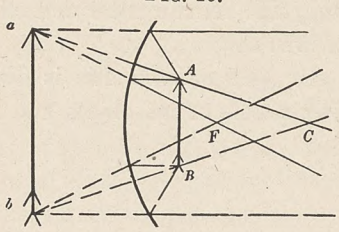
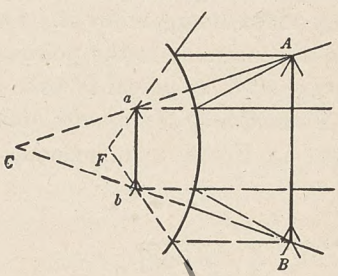


FIG. 11.



than the principal focus of the mirror; so that, object and image being both on the same side of the centre of curvature, the image is erect.

The relative size of the image formed by a spherical mirror is proportioned to its relative distance from the centre of curvature of the spherical surface. Thus, in Figs. 9, 10, and 11 (the lettering being the same in all) we have *ABC* and *abC* similar triangles, in which

$$ab : AB :: aC : AC.$$

DIOPTRICS, OR THE REFRACTION OF LIGHT.

Light-waves move at different rates in different dioptric media. We have already seen that the rate of movement in vacuum is 186,380 miles per second. Taking as unit the length of time it requires to go a certain distance in vacuum, the following table gives the length of time it would require to go the same distance in the substances named. This number indicating the relative length of time it takes light to travel a certain distance in a given substance is called the *index of refraction* of the substance. It is customary and convenient in ophthalmology to take the index of refraction of air as unit; but, since this differs from that of vacuum only in the fourth decimal place, the difference may for all practical purposes be disregarded.

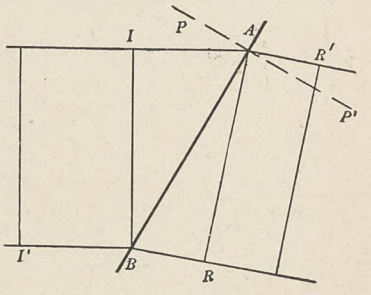
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Substance.	Index of Refraction.
Vacuum	1.
Air	1.000294
Water at 0° Cent.	1.3330
Water at 40° Cent.	1.3297
Alcohol	1.372
Canada balsam	1.532
Aqueous humor	1.3365
Vitreous humor	1.3365
Cornea	1.3365
Crystalline lens	1.39 to 1.43
Crown glass	1.51 to 1.54
Flint glass	1.55 to 1.72
Rock crystal	1.55 to 1.57
Diamond	2.47 to 2.75

It is common to speak of differences of index of refraction as differences of "density." But index of refraction must not be confused with specific gravity, which is usually meant when the word "density" is used, and with which it has no direct or constant relation. For instance, water, with a specific gravity of 1, has an index of refraction of 1.333, while alcohol, with a specific gravity of only 0.728, has an index of refraction of 1.372.

If we suppose a succession of light-waves passing from one medium having a lower to another having a higher index of refraction, as from air into glass, the distances travelled by each wave-front in a unit of time will be the reciprocals of the indexes of refraction; that is, while a wave-front is passing a distance $\frac{1}{1}$ in the air, it passes only $\frac{1}{1.53}$ (or a little less than two-thirds the distance) in the glass. If all parts of each wave-front enter the glass at the same time,—that is, if the wave-fronts are parallel (the rays perpendicular) to the dioptric surface,—their direction is unaltered by the passage. When, however, the wave-fronts strike the dioptric surface obliquely, one portion still moving in the first medium, while another part of the same wave-front has passed into the second medium, the slower movement in the latter causes a change of direction in the wave-fronts and a change in the direction of the movement of the light, since this is always perpendicular to the wave-fronts. Such change of direction is called the *refraction of light*. The general nature and extent of such a change of direction are indicated in Fig. 12. AB represents a dioptric surface separating air and glass; IB, a wave-front falling on the glass from the air; AR, a wave-front passing in the glass; IA and $I'B$, incident rays, and BR and AR', refracted rays; and PP', a perpendicular to the dioptric surface at A. Since the light travels in the glass only $\frac{1}{1.53}$ as far as in the

Fig. 12.



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air, $\frac{BR}{1} = \frac{IA}{1.53}$. But since the rays are perpendicular to the wave-fronts, ABI and ABR are right-angled triangles in which IBA is the angle of incidence and BAR the angle of refraction. Taking the common side AB as radius, we have IA = sine ABI and BR = sine BAR. Hence

$$\frac{\text{sine of the angle of incidence}}{1.53} = \frac{\text{sine of the angle of refraction}}{1},$$

or

sine of the angle of incidence : sine of the angle of refraction : : 1 53 : 1.

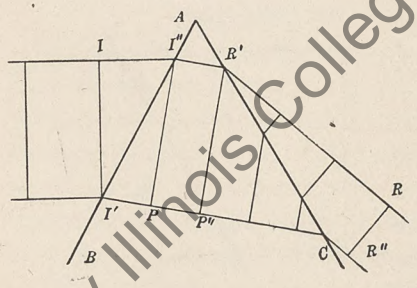
In general, this relation is thus stated : *The sine of the angle of incidence is to the sine of the angle of refraction as the index of refraction of the medium into which the light passes is to the index of refraction of the medium from which it passes.*

If we consider the angle of incidence between the ray IA and the perpendicular PP', and the angle of refraction between the ray AR' and the same perpendicular, it appears that *the ray is bent towards the perpendicular on passing from a less refracting to a more refracting medium.* If, on the other hand, the light is supposed to pass from the glass into the air, it is evident that *the ray is equally bent from the perpendicular in passing from a more refracting to a less refracting medium.*

Refraction by a plate of glass with parallel surfaces, when held in the air, is equal at both surfaces, because, the angle of incidence at the second surface being the same as the angle of refraction at the first surface, the angle of refraction at the second surface must be equal to the angle of incidence at the first surface, and the direction of any ray after leaving the second surface is parallel to the direction of the same ray before reaching the first surface.

Refraction by a Prism.—When a portion of a refracting medium is bounded by two plane surfaces inclined towards one another, it is called a prism, and by passing through it the directions of the wave-fronts and rays are permanently altered. This is illustrated in Fig. 13, in which AB and AC represent the bounding surfaces of a prism of glass, or other medium, more refractive than the air by which it is surrounded. The edge in which these surfaces intersect at A is the *apex* or *edge* of the prism, and the angle at which they meet is the *refracting angle.* The thickest part of the prism BC is the *base.* II' shows the direction of the wave-front before entering the prism, $I''P$ its direction while in the prism, and RR'' its direction after leaving the prism. II'' shows the direction of a ray before entering the prism, $I''R'$ its direction in the prism, and $R'R$ its direction after leaving the prism. Obviously,

FIG. 13.

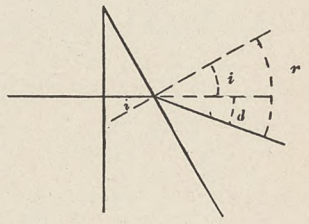


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whatever the original direction of the wave-front, the part of it that goes through the thicker part of the prism will, on the whole, be more retarded than the part that goes through the thinner part of the prism. It will be turned towards the base of the prism, with a corresponding change in the direction of the ray. The amount of this change of direction is the *angle of deviation*. The amount of deviation produced by a prism varies with the angle at which the incident ray strikes it. When the angle of the incident ray with the first surface is just equal to the angle of the refracted ray with the second surface, and the ray within the prism is perpendicular to the plane bisecting the refracting angle, this deviation is the least, and is called the *minimum deviation*. This position of the prism is called the *position of minimum deviation*. When the strength of a prism is spoken of, it is generally understood, unless otherwise indicated, to mean its power of minimum deviation. The effect of rotating a prism from its position of minimum deviation can be readily observed by looking through it at a line parallel to its edge, and noting the change in the apparent position of the line produced by rotation. This change of strength by rotation is due to the fact that the nearer an angle approaches to 90° the more is it increased for a given increase of its sine, and rotation of the prism from the position of minimum deviation, while it may make the angle of incidence less at one surface, always makes it greater at the other, and the gain to the larger angle always causes a greater increase of deviation than the equal diminution occasioned by the reduction of the smaller angle. For the same reason a strong prism has more deviating power in proportion to its refracting angle than a weak prism. Thus, a prism having a refracting angle of 8° will cause a minimum deviation of 4° 16′, while one having a refracting angle of 80° causes a deviation of 79° 4′. The latter prism, with ten times the refracting angle of the former, has over eighteen times its refracting power.

To ascertain the effect of a prism upon a ray of light passing through it, we must for most positions of the prism calculate the deviation produced both on entering and on leaving the prism, and get the algebraic sum of the two. When, however, the ray passes within the prism perpendicular to one of its surfaces, it is refracted only at the other surface, and it is only necessary to determine its deviation there. Thus, in Fig. 14, suppose the incident ray perpendicular to the surface through which it enters. It will be refracted only at the surface of exit, where the angle of incidence i will (because the sides of the two angles are mutually perpendicular) be equal to the refracting angle of the prism. If the prism be of ordinary optical glass with an index of refraction of 1.53, we have, letting r represent the angle of refraction,

FIG. 14.



$$\sin i \times 1.53 = \sin r.$$

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Suppose the refracting angle of the prism to be 10°. The sine of 10° = 0.1736. Hence

$$\sin r = 0.1736 \times 1.53 = 0.2656,$$

which is the sine of 15.4°, the angle of refraction. The angle of deviation, $d = r - i$,

$$15.4 - 10 = 5.4°,$$

the angle of deviation for a prism having a refracting angle of 10°.

When it is desired to ascertain its minimum deviation, a prism may be regarded as made up of two equal parts, in each of which the refraction is all at one surface, as in the preceding example. Calculating the deviation for one of these halves, and doubling it, gives the deviation of the whole prism.

If, in the above example, with the refraction all at one surface, we had taken, instead of 10°, a refracting angle of 40° 49′, the angle of refraction would have been 90° ; that is, the ray after refraction would have remained in the plane of the surface and would not have escaped from the prism. This is called the *limiting angle.* Light striking the surface with a greater angle of incidence than this does not pass out, but is *totally reflected* within the prism. If we took a prism of double this refracting angle, or 81° 38′, no light could pass through it.

When rays fall upon a prism parallel, having all the same angle of incidence, they continue parallel after refraction. When, however, they fall upon the prism divergent or convergent, having different angles of incidence, they are not equally refracted, but their divergence or convergence is slightly altered. This alteration is, however, for ordinary ophthalmological prisms so slight when the rays fall at a small angle of incidence that it may for practical purposes be disregarded. For a more complete account of prisms, the reader is referred to the article "Prisms and Prismometry." Only such matters have been discussed here as are related to refraction by lenses.

Dispersion of Light.—We have thus far spoken of the index of refraction as though each dioptric medium had but one fixed index. But not only does this index vary with changes of density that accompany changes of temperature, but it is different for light of different wave-lengths. In vacuum, all kinds of light appear to travel at the same rate ; but in most dioptric media they are unequally retarded, and there seems to be no constant ratio between the indexes of refraction for light of different colors in different substances. Commonly the light with short wave-lengths (near the violet end of the spectrum) is most retarded and most refracted ; but by some substances, as the vapor of iodine, red light is more retarded and refracted than blue.

The following table gives the indexes of refraction of crown and flint glass for light of different colors, the letters giving Fraunhofer lines that exactly locate the light in the spectrum :

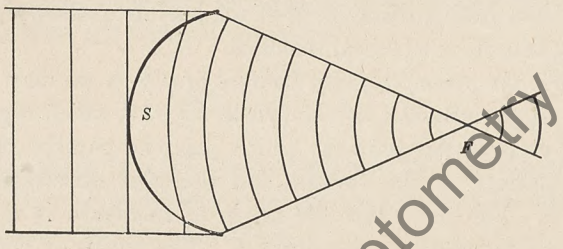
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Color of Light.	Fraunhofer Line.	Crown Glass.	Flint Glass.
Red	B	1.5136	1.6157
Yellow	D	1.5171	1.6224
Green	E	1.5203	1.6289
Blue	F	1.5231	1.6347
Violet	H	1.5328	1.6562

These differences of refractive index cause the notable separation or *dispersion of light* of different colors when strongly refracted by prisms or lenses, giving rise to *chromatic aberration*, which requires very careful correction in such optical instruments as the telescope and the microscope, and which interferes somewhat with the use of the strongest ophthalmic prisms and lenses.

Refraction by Convex Spherical Lenses.—When light passes from one dioptric medium to another through a spherical surface, in such a way that a part of each wave-front is in one medium while a part is in the other medium, the shape of the wave-fronts and the direction of the rays along which they move are changed. Thus, in Fig. 15 let *S* represent a spherical surface separating two media and *convex towards the less refractive medium* from which comes the light, the wave-fronts being represented by the parallel

FIG. 15.



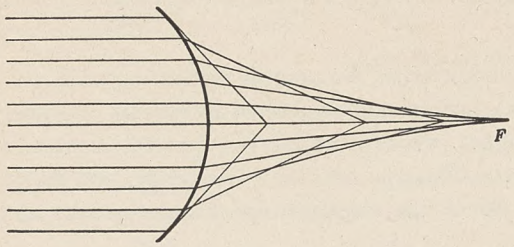
lines. The centre of each wave-front first enters the more refractive medium and is retarded, while the parts on either side passing on at the more rapid rate get ahead of it, so that when the whole wave-front has entered the second medium it is concave forward, and its motion perpendicular to the direction of the wave-front causes it to concentrate to a single point *F*, its centre of curvature, after which it again begins to spread out.

In Fig. 15 the representation has been as though the wave-front, after passing the surface, were perfectly spherical in form, concentrating accurately to a single point. But the passage through a spherical surface does not effect this. Only the part of the wave-front near the centre of the lens—the part where the angle of incidence is very small—sufficiently approximates the spherical form to be so regarded. The more peripheral portions of the wave-front are really bent round too much, so that their centres of curvature lie, and tend to concentrate, in front of the centre for the middle portion. What really happens is shown in Fig. 16, where, for simplicity, only the rays are represented. They are supposed to pass parallel in the more refractive medium.

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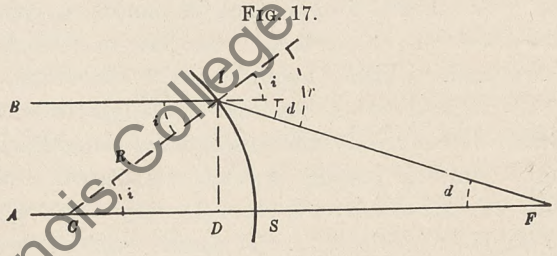
The rays passing through the central part of the surface are concentrated to practically a single point F, but others passing through the periphery are concentrated at various points nearer the surface. This failure of a spherical surface accurately to concentrate the rays that fall upon it obliquely is called *spherical aberration*, or *monochromatic aberration*, in contradistinction to chromatic aberration due to the dispersion of light. Since the whole value of the lens in physiological optics is to cause the rays of a pencil all to converge towards or diverge from a certain point, the whole optical theory of lenses has to be based on the assumptions that the lens surface includes only a very small portion of the sphere of which it is a part, and that the rays fall upon it nearly perpendicular to its surface. Working, then, under the above assumptions, the point at which the pencil of light is concentrated is called a *focus*. The focus for a pencil of parallel rays (flat wave-fronts) is called the *principal focus* of the lens, and its distance from the lens its *principal focal distance*, commonly spoken of as the focal distance.

FIG. 16.



To ascertain the principal focal distance of a lens, we may consider what happens to a single refracted ray, shown in Fig. 17, which represents a portion of a spherical surface through which pass two parallel rays AF, going through the centre C of the surface, and therefore unrefracted, and BIF refracted at I. For the latter the angle of incidence is i, the angle of refraction r, and the angle of deviation d. The radius of curvature of the surface is R, and the focal distance SF is f. Let the index of refraction for the first medium be n, and for the second medium n'. The accurate

FIG. 17.



focussing of light by a spherical surface is possible only when the angles i, r, and d are so small that we may consider them as identical with their sines, and DS is so short that it may be disregarded, leaving FD or IF equal to FS. We have, then, in the right-angled triangles IDC and IDF, $ID = CI \times \sin i = \mathrm{R} \times \sin i$, and $ID = IF \times \sin d = f \times \sin d$. Hence

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$$R \times \sin i = f \times \sin d.$$

$$f = R \frac{\sin i}{\sin d}.$$

But $d = r - i$, or $\sin d = \sin r - \sin i$, and, by the general law of refraction,

$$n \times \sin i = n' \times \sin r.$$

$$\sin r = \frac{n}{n'} \sin i.$$

Hence

$$f = R \frac{\sin i}{\sin r - \sin i}.$$

$$f = R \frac{\sin i}{\frac{n}{n'} \sin i - \sin i} = R \frac{1}{\frac{n}{n'} - 1}. \qquad (A)$$

Now, if we have the first medium glass and the second air, we have $n = 1.53$ and $n' = 1$; and the focal distance of a glass lens in air, where the refraction was all at one surface (a plano-convex lens, with rays perpendicular to the plane surface), would be

$$f = \frac{R}{\frac{1.53}{1} - 1} = \frac{R}{.53}.$$

For a biconvex lens, by which the light is refracted equally on entering and on leaving the lens, the formula would be

$$f = \frac{R}{.53 \times 2} = \frac{R}{1.06}. \qquad (B)$$

The focal distance of a lens is directly proportional to the radius of curvature, and inversely proportional to the difference between the refractive indexes of the two media, or its refractive power.

If we designate the refractive power or "strength" of a lens by S, and its focal distance by F, we have

$$S = \frac{1}{F}; \text{ or } F = \frac{1}{S}. \qquad (C)$$

When lenses are combined so as to add their strengths, as $S + S' + S''$, etc., we can express the same thing thus:

$$\frac{1}{F} + \frac{1}{F'} + \frac{1}{F''}, \text{ etc.}$$

Or we may conceive a lens strength S as made up of $S' + S''$, in which case

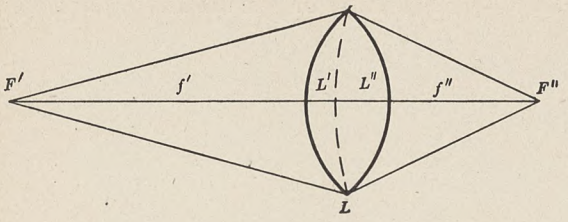
$$\frac{1}{F} = \frac{1}{F'} + \frac{1}{F''}. \qquad (D)$$

Conjugate Foci.—Formula (D) indicates the relations between the different focal distances of a lens. Let Fig. 18 represent a lens L, whose principal focal distance is f, and which, on receiving rays from F', focusses them at

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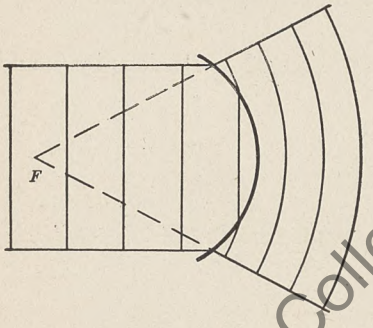
F''. The lens L may be regarded as made up of two parts, L' having a principal focal distance f', and L'' having a principal focal distance f''. Rays diverging from F' are rendered parallel by L', and the parallel rays are converged to F'' by L''. Or, conversely, rays from F'' are rendered parallel by L'' and focussed at F' by L'. F' and F'' are called *conjugate foci*, and their relation to the principal focus of the lens is expressed by Formula (D). It is evident that for each value of f' there is a corresponding value for f''. As f' diminishes f'' increases, until when f' equals f, f'' equals infinity. The focus conjugate to the principal focus is at an infinite distance. When f' is twice f, f'' is also twice f; that is, when the conjugate foci are the same distance from the lens, this distance is double the principal focal distance of the lens. When f' becomes less than f, f'' becomes negative and diminishes with f'; the conjugate foci are both on the same side of the lens, and one of them is a virtual focus. Given the principal focal distance and one conjugate focus, we can by the formula find the other conjugate; or given both conjugate focal distances, we can find the principal focal distance.

Fig. 18.



Refraction by Concave Lenses.—If light passes from one dioptric medium to another through a spherical surface *concave towards the less refractive medium*, the effect upon it is that represented by Fig. 19. The central portion of each wave remains in the less refractive medium, moving at its previous rate after the peripheral portions have entered the more refractive medium and are being retarded by it. This allows the central portion of each wave to get ahead of the peripheral portions, so that when the whole wave-front has entered the second medium it is convex forward, as though the light had emanated from a point F, the centre of curvature of the successive waves after refraction. All rays, as those shown in the figure, after refraction diverge from the same point. This point from which the light after refraction appears to emanate is a *focus* of the concave lens. Since the light does not really pass through it, it is called a *virtual focus*, in contrast with a *real focus*, like F in Fig. 15, through which the light will actually pass. As for convex lenses, the distance of the focus from the lens is the *focal distance*, the focus for rays previously parallel is the *principal focus*, and its distance from the lens is the *principal focal distance*. The formulas given for convex lenses, with

Fig 19.

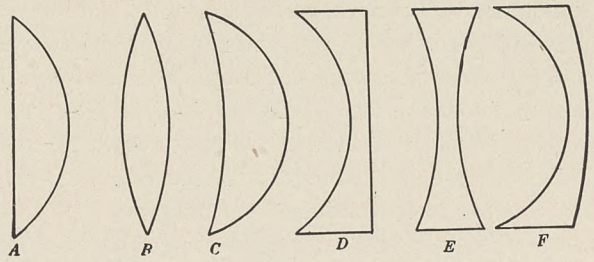


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the needful changes of signs, the existence of spherical aberration, and the relations of conjugate foci, all hold for concave lenses.

Different Forms of Lenses.—Six general classes of lenses differing in their essential forms are illustrated in Fig. 20. The representation is of lenses of about the same strength.

FIG. 20.



A. Plano-convex: One side convex, the other plane.

B. Double convex: Both sides convex. When both sides are equally convex, as represented in the figure, the lens is called *biconvex.*

C. Concavo-convex: One side concave, the other more convex.

D. Plano-concave: One side concave, the other plane.

E. Double-concave: Both sides concave. When they are equally concave, as in the figure, the lens is called *biconcave.*

F. Convexo-concave: One side convex, the other more concave.

Either *C* or *F* is called a *meniscus*, or periscopic lens.

In each lens there is a certain point where its bounding surfaces are parallel. This is called the *optical centre* of the lens. Lenses thickest at the optical centre act as convex lenses, and those thinnest at the optical centre as concave lenses. Any lens may be regarded as a series of prisms growing progressively stronger from the optical centre to the edge of the lens. For a convex lens the prisms have their bases all turned towards the centre of the lens; for a concave lens their bases are turned from the centre. Hence the former are *converging*, the latter *diverging* lenses.

To ascertain the total effect of any lens, it is needful to consider the refraction at both surfaces. Thus, in the plano-convex lens we can consider the refraction of the plane surface as zero, and the total converging power of the lens to be that of its convex surface. A double convex lens is to be regarded as a combination of two plano-convex lenses of the appropriate curvatures, the sum of whose strengths gives the strength of the whole lens. A concavo-convex lens, however, is equal to a combination of a plano-concave lens with a plano-convex lens, and the total effect is the excess of the converging over the diverging action. Concave lenses of various forms are to be regarded in the same way.

The Numbering of Lenses.—At first, lenses were numbered according to the radius of curvature in inches of the lens surface. But lenses having different forms would by this plan be known by different numbers, although

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they might have the same optical effect. On this account convex lenses of other forms came to be known by the number of the equivalent biconvex lens, and other concave lenses by the number of the equivalent biconcave lens, this number being the number of inches in the radius of curvature of the equally curved surfaces.

It will be noticed that for a biconvex lens Formula (B) gives the focal distance as the radius of curvature divided by 1.06. Hence the numbers of lenses on the old plan closely approximated the focal distances of the lenses in inches. For people using the English inch as a unit of distance this approximation was still closer. The first sets of trial-lenses were chiefly made in Paris, and numbered by the radius of curvature in Paris inches, and the Paris inch is 1.066 times longer than the English inch. Hence the number of Paris inches in the radius of curvature almost exactly coincided with the number of slightly shorter English inches in the slightly shorter focal distance.

To the user of lenses the radius of curvature of its surfaces is not a matter of direct importance. The things which are of direct and principal importance are the strength and focal distance of the lens; hence the numbers of lenses came to be regarded as indicating their respective focal distances. We have seen—Formula (C)—that the strength of a lens is the reciprocal of its focal distance. If the focal distance be expressed in a whole number, whether of inches or centimetres, the strength is expressed by a fraction,—one divided by that number. In working with lenses, it is very frequently necessary to add and subtract their strengths or refractive powers, and any system of numbering by focal distances compels the addition and subtraction of vulgar fractions, which have to be reduced to a common denominator.

To avoid the difficulty of so working with vulgar fractions, it was necessary to number lenses according to their strengths, using only whole numbers or fractions having a common denominator.

For this purpose the refracting power of a metre-lens—a lens having a focal distance of one metre—was chosen as the unit, and was called a *dioptre;* and the system of numbering based on this is called the *metric* or *dioptric system.* The interval of a whole dioptre being too great for a complete series of ophthalmic lenses, intermediate lenses were introduced at regular intervals of one-quarter dioptre and numbered in decimals, so that their addition or subtraction is as simple as that of whole numbers. Later, when additional lenses were added at irregular intervals, the writer urged that, in "adding to the metric series, the simplicity of the system should be carefully preserved by making the interval one-eighth dioptre,—an exact division of the interval previously adopted."[1] This plan has since been generally followed.

While in practical work it is commonly the strength of lenses which we

[1] Transactions of the Amer. Ophthalmol. Soc., 1887, vol. iv. p. 596.

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wish to add to or subtract from, it is sometimes necessary to add to or subtract from the focal distance. This it is easier to do for lenses numbered by their focal distance, since by the metric system the focal distance is always a fraction, one divided by the strength. It is therefore worth while to have both sets of numbers in mind, and to be able to convert the one into the other. Having the dioptric number, by dividing it into 40 or 39 (there are 39.37 inches in a metre) we obtain the number according to inches of focal distance; or having the number of inches focal distance of a lens and dividing it into 39 or 40, we get the number of the lens in the dioptric system. The following table gives the numbers for a fairly complete series of trial-lenses with their focal distances and the nearest equivalent lens of the older series. It will be noted that the stronger lenses are separated by longer intervals because they are less frequently required, and intermediate strengths can be gained by combinations, or the effect secured by varying the distance of the lens from the eye (see Correction of Hyperopia).

Number by Dioptres.	Focal Distance in Millimetres.	Focal Distance in English Inches.	Number in Old Series.
0.12 (0.125)	8000	315.	. .
0.25	4000	157.5	144
0.37	2667	105.	100
0.50	2000	78.7	72
0.62	1600	63.	60
0.75	1333	52.5	48
0.87	1143	45.	. .
1.	1000	39.37079	40
1.12	889	35.	36
1.25	800	31.5	30
1.37	727	28.6	. .
1.50	667	26.2	24
1.75	571	22.5	. .
2.	500	19.7	20
2.25	444	17.5	18
2.50	400	15.7	16
2.75	364	14.3	14
3.	333	13.1	. .
3.25	308	12.1	12
3.50	286	11.2	11
4.	250	9.8	10
4.50	222	8.7	9
5.	200	7.9	8
5.50	182	7.2	7
6.	167	6.5	6
7.	143	5.6	$5\frac{1}{2}$
8.	125	4.9	5
9.	111	4.4	$4\frac{1}{2}$
10.	100	3.9	4
11.	91	3.6	$3\frac{1}{2}$
12.	83	3.3	. .
13.	77	3.	3
14.	71	2.8	$2\frac{3}{4}$
15.	67	2.6	$2\frac{1}{2}$
16.	62	2.4	. .
17.	59	2.3	$2\frac{1}{4}$
18.	55	2.2	. .
19.	52	2.1	. .
20.	50	2.	2

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Axes, Nodal Points, and Images.—A straight line passing through the centres of curvature of both surfaces of a lens, and therefore perpendicular to those surfaces, is called the *principal axis* of the lens. A ray of light passing in the direction of the principal axis is not refracted at either surface. All other rays are refracted; but from any point outside of the principal axis one ray may fall on the lens in such a way that, although it strikes the surfaces obliquely, the two surfaces are parallel at the points at which it enters and leaves the lens, so that the lens has upon it the effect of a plate of glass with parallel sides. The direction of the ray after leaving the lens is parallel to its direction before entering the lens. Such a ray is called a *secondary axis.* A point upon the primary axis towards which such a ray is directed before entering the lens is called the *first nodal point.* The point upon the primary axis from which it passes after leaving the lens is the *second nodal point.* All the secondary axes of a lens pass towards and from the same nodal points. Their location is shown for the different forms of convex lenses in Fig. 21, and for the different forms of concave lenses in Fig. 22. In each

FIG. 21.

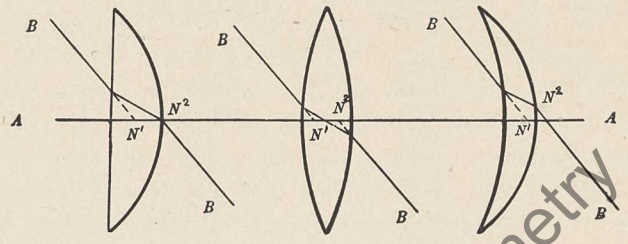


FIG. 22.

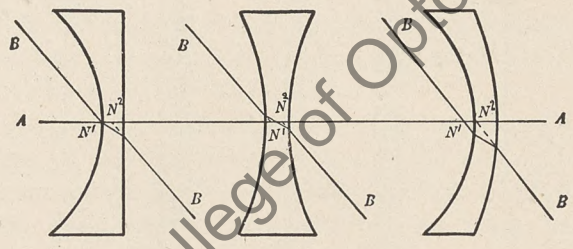
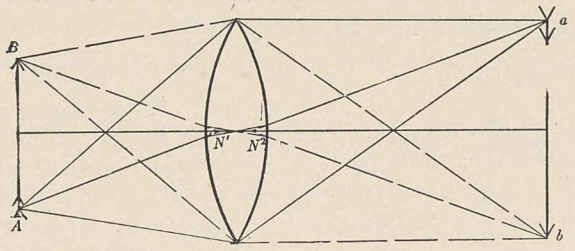


figure AA is the primary axis and BB a secondary axis of the lens, and N^1 the first and N^2 the second nodal point for rays passing from left to right. Where the medium through which the light passes before entering and after leaving the lens is the same, the nodal points are also the *principal* points of the lens. If through each of the principal points a plane be passed perpendicular to the primary axis, these planes will be the *principal planes.* Any ray passing before entering the lens towards a certain point in the *first principal plane* will, after leaving the lens, pass through or from a point in the *second principal plane,* similarly situated with reference to the primary axis.

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The focus for a pencil of rays coming from any point on the primary axis will be another point on the primary axis. The focus for rays from a point on any secondary axis will be another point on that same secondary axis. From each luminous point of an object passes a secondary axis, on which, at a conjugate focus, are focussed the rays emanating from it that pass through the lens. Each point of an object thus has its image, and the assemblage of these images forms the image of the object. Fig. 23 illus-

FIG. 23.



trates this for a convex lens, the object AB being situated farther from the lens than its principal focus. In this case the object and the image are *on opposite sides of the nodal points*, and therefore *the image is inverted with reference to the object.* The image is a *real image.* Fig. 24 represents the formation of an image by a convex lens when the object is closer to the lens than its principal focus, and the image and the object, therefore, are on the same side of the nodal points. In this case the image is *virtual and erect.*

FIG. 24.

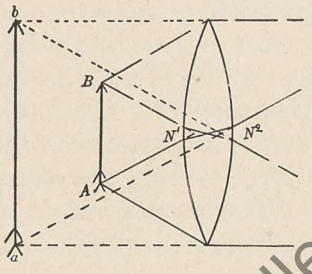
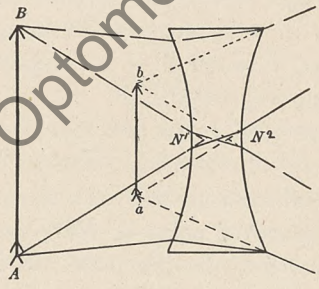


FIG. 25.



In Fig. 25 is represented the formation of an image by a concave lens. Here also the object and the image are on the same side of the nodal points, and the image is erect and virtual.

The relative sizes of the object and the image are proportioned to their distances from the nodal points: thus, in Figs. 23, 24, and 25 we have the similar triangles ABN^1 and abN^2 (their sides being mutually parallel), in which

$$AN^1 : N^2a :: AB : ab.$$

It may be noted that in Fig. 24 the image ab is farther from the nodal point than the object AB; therefore the image is larger than the object.

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But in Fig. 25 *ab* is nearer the lens than *AB:* the image is smaller than the object. Therefore Fig. 24 represents a *magnifying* and Fig. 25 a *minifying* lens.

Refraction by a Cylindrical Lens.—A lens may be bounded by curved surfaces other than spherical. Of especial interest in ophthalmology is a lens one or both surfaces of which are segments of a cylinder or cylinders. Such a lens is called a *cylindrical lens.* Cylindrical lenses may have any of the general forms enumerated for spherical lenses, but are commonly made plano-convex and plano-concave. These forms and the way in which they refract light are represented in Figs. 26 and 27.

FIG. 26.

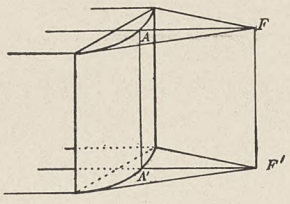
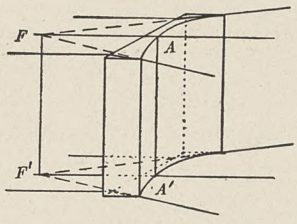


FIG. 27.



The line AA' passing in the centre of the cylindrical surface, parallel to the direction of the axis of the cylinder of which the surface is a part, is called the *axis* of the cylindrical lens. The lens in any plane perpendicular to the axis has a curvature and a refractive power similar to those of the spherical lens in all directions, but in any plane parallel to the axis it has no refractive power.

Thus, in Fig. 26, suppose parallel rays to fall on the lens. Of those lying in a plane passed through A perpendicular to the axis, the ray passing through A is not refracted, and the other rays are bent towards it so that they meet in F. So, too, in the plane $A'F'$ the rays are brought to a focus at F'; but the rays in the one plane are not bent towards or from the rays in the other plane. The same is true of all intermediate planes perpendicular to the axis, the rays in each being brought to a focus in a corresponding point of FF'; so that the line FF' is the focus of the cylindrical lens. In the same way the concave cylindrical lens represented in Fig. 27 refracts the rays that pass through it, except that, being a concave lens, it causes the rays to diverge as though they had come from the line FF', its virtual focus.

As to refraction by a cylindrical lens in the plane perpendicular to its axis,—the plane in which it has a lens action,—what has been said in connection with spherical lenses will apply. Its power of accurately focussing rays is similarly confined to those which fall nearly perpendicular to its surface; its *principal focus* and *focal distance* have the same relation to it and to its strength. The relation of its *conjugate foci* to the principal focus is the same, and the *system of numbering* is the same. Its *primary* and *secondary axes* and *nodal points* have the same relations; but there are a

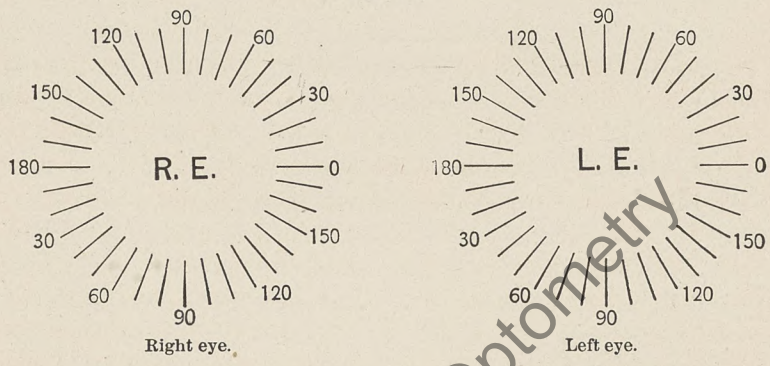
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primary axis, two nodal points, and a full system of secondary axes in each plane perpendicular to the *cylinder axis*, those of one plane being similar to all the others. The formation of *images*, the determination of their size, and their reversal are the same as for spherical lenses, except that they are confined to the one plane.

The fact that the cylindrical lens acts only in one plane makes it necessary always to recognize in connection with it the direction in which it is turned. This is done in ophthalmic work by describing an imaginary circle in the plane of the face around each pupil as a centre, and laying this off in degrees from 0 to 180, the two halves of the circle being similarly numbered. Trial-frames, test-cards, etc., are then graduated to conform to this circle.

Different systems of graduation have been proposed. That in most general use in America, when viewed from in front, as by the surgeon facing the patient, conforms to the graduation of the circle followed in other departments of mathematics. It is shown in Fig. 28.

FIG. 28.



Starting with 0 at the right of the horizontal diameter, it goes upward, 90° being vertical, and over to 180° at the left of the horizontal diameter. It is the same for both eyes. Other plans of graduation have been proposed to make the numbering symmetrical with reference to the vertical meridian of the eye or the median plane of the body. Harlan would reverse the direction of graduation for the left eye, making it start from the nasal end of the horizontal meridian for both eyes and go upward.[1] Knapp suggests counting from the upper end of the vertical meridian down the nose to its lower end, from 0° to 180° for each eye.[2] Snellen, followed by Landolt and many other European surgeons, starts from the upper extremity of the vertical meridian, and numbers from 0° to 90° both to the nasal and to the temporal side.

To ascertain the Strength of a Lens.—For a convex lens the strength may be ascertained by noting at what distance it focusses parallel rays, as

[1] Archives of Ophthalmology, vol. xxii. p. 250.

[2] Loc. cit.

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the rays of light from the sun. Or this may be calculated from the position of conjugate foci, Formula (D), as a point of light on one side of the lens and its image on the other side, the distances of which can readily be measured. The strength of a concave lens may be ascertained by combining it with a stronger convex lens of known strength and ascertaining how much that strength is diminished thereby. When the index of refraction of the glass is known, the strength of the lens can be learned by measuring the curvature of its surfaces.

The common practical method, however, is by finding what lens of the opposite kind is required to neutralize its optical effect. When a convex lens is held before the eye, but not beyond its focal distance, and moved from side to side, objects seen through it appear to move in an opposite direction. When the same is done with a concave lens, objects appear through it to move in the same direction as the lens. When a convex lens is closely applied to a concave lens of equal strength, no such apparent movement occurs. To ascertain, then, the strength of a convex lens, it is only needful to ascertain by trial the number of the concave lens from the trial-case which neutralizes it. In the same way the strength of a concave lens is known by that of the convex lens which just neutralizes it. Spherical lenses are to be neutralized by spherical lenses. Cylindrical lenses may be neutralized by cylindrical, care being taken to have their axes turned the same way; or they and combinations of spherical and cylindrical lenses may be neutralized by one spherical in the direction of the axis of the cylinder, and then by a different spherical at right angles to that axis: the difference between these gives the strength of the cylindrical lens. For neutralization, plano-convex and plano-concave lenses are better than the biconvex and biconcave lenses often found in trial-cases. The superiority of the former is very marked for strong lenses, because with them the neutralizing surfaces may always be directly applied to one another.

To determine the Axis of a Cylindrical Lens.—On account of its influence on the nodal points of the eye (see Astigmatism, latter part of this article), a cylindrical lens held before the eye changes the apparent direction of all lines seen through it that are not parallel to its cylinder axis or perpendicular to the same. To determine the axis, hold a cylindrical lens so as to see through it a part of some straight line, as a window-sash, the continuation of which can be seen above and below the lens. Then turn the lens in its own plane until the part of the line seen through it appears continuous with the parts above and below. The axis of the lens is then parallel to this line or perpendicular thereto.

To find the Optical Centre of a Lens.—Hold it as when fixing the direction of a cylinder axis, and when the line seen through it appears continuous with the parts above and below it, draw on the lens a line where the line looked at appears to cross it. Turn the lens so that the line drawn on it will be perpendicular to the line looked at. Their apparent intersection is the optical centre of the lens.

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Many practical points with reference to ophthalmic lenses and their mounting cannot be discussed here. The reader is referred to the little work, "Spectacles and Eye-Glasses: their Forms, Mounting, and Adjustment," by R. J. Phillips, M.D., for a fuller account of the subject.

THE REFRACTION OF THE EYE.

The difference between bare light-perception and the full normal vision of man consists in ability to receive distinct visual impressions from different objects, and rests on the power of the eye to assort the light entering it. The eyeball may be defined as an apparatus to assort light and sustain the part of the nervous system specialized for the reception of luminous impressions in a favorable position to receive those of assorted light. Under the conditions of perfect vision, light entering the pupil is so assorted that all coming from a single luminous point of the object looked at is concentrated to make its impression on a single point of the retina. This assorting of the light is effected by the action of the dioptric surfaces and media of the eye, resembling that of a convex lens.

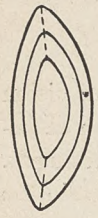
Light entering the eye passes from air having an index of refraction of 1, to the corneal tissue having an index of refraction of 1.3365, through a surface convex towards the air. The rays of an incident pencil are by this passage rendered relatively convergent. Continuing their course, they pass through the aqueous humor, which has, however, the same index of refraction as the cornea, and is therefore, as regards its dioptric qualities, a continuation of that medium. Reaching the anterior surface of the crystalline lens, the light again passes from a less refractive to a more refractive medium, through a surface convex towards the former, and thus its rays are rendered still more convergent. Of the index of refraction of the lens and its effect on the refraction of the eye more will be said presently. At the posterior surface of the lens the light passes from the more refractive lens-substance into the vitreous having the same refractive index as the cornea and aqueous, but again through a surface convex towards the less refractive medium, so that the rays are still farther converged. They then pass on directly through the vitreous and superficial layers of the retina to focus (in the properly proportioned or emmetropic eye) in the percipient layer, the slight variation of refractive index in the retina being practically nullified by the comparative flatness, and nearness to the focus, of its surface.

Returning to the refraction of light by the crystalline lens, we find that it is not a simple matter of refraction at two surfaces. The index of refraction varies from layer to layer, increasing from its surfaces to its centre; and as light passes from one layer of the lens to another it is refracted in correspondence to the slight change of refractive index. The surfaces separating the layers being, like the surfaces of the lens, always convex towards the less refracting medium, the change is in each instance towards greater convergence. To determine by exact calculation these minute changes of direction that occur to the rays during their whole

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passage through the lens is manifestly impossible. We have not methods for accurately determining the index of refraction of any single layer or of accurately measuring its thickness during life. The best we can do is to determine what refraction will, on the whole, most nearly represent the effect of the average crystalline lens.

Fig. 29.



For this purpose physiologists have agreed to consider the lens as though it were composed of three layers having each its own index of refraction, different from those of the other layers, but uniform through its whole extent. These three parts are called nuclear, intermediate, and external. Their relations are shown in Fig. 29.

The mean index of refraction for each of these different layers varies considerably, as determined in different eyes by different observers, but approximates for the

External layer	1.40
Intermediate layer	1.42
Nucleus	1.43

This division of the lens into three layers has been used chiefly as a basis from which to calculate the index of refraction and curvatures of surface which would give a refractive effect equal to that of the crystalline lens as it is, if that lens possessed the same index of refraction throughout. From his later calculations, Helmholtz reached the conclusion that the equivalent of the crystalline lens having a curvature on its anterior surface of ten millimetres' radius and on its posterior surface a curvature of six millimetres' radius should have an index of refraction of 1.4371. (He had earlier adopted an index of 1.4545.)

It will be noted that this index for the whole lens is not a mean or average of the indexes of the different portions of the lens, but is higher even than the observed index of the nucleus. The reason for this will appear from a careful examination of Fig. 29. We have in the crystalline, first, a double convex lens, the nuclear portion, having surfaces that are more convex than the surfaces of the whole lens; second, in front and behind this are a series of menisci which are thinnest at the centre, and would, therefore, if acting alone, tend to diverge the rays passing through them. These menisci partially neutralize the effect of the double convex nuclear portion. If these menisci had the same index of refraction as the nuclear portion, they would neutralize its effect to a certain extent, and would leave the total effect of the lens that of a double convex lens having the curvatures of the crystalline with the index of refraction of the nucleus. These menisci, however, have a lower index of refraction, and hence have less power to neutralize the converging effect of the nuclear part, so that the total converging effect of the lens is left greater than it would be were the index of refraction uniformly that of the nucleus. Now, as we adopt the curvatures of the actual crystalline for the curvatures of the equivalent lens

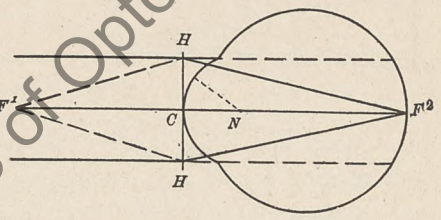
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possessing this stronger converging power, the only thing to be done to make it properly equivalent is to assign it a higher index of refraction. Briefly, the convergence of rays accomplished by the crystalline is not done by a lens having its exterior curves, but by the more convex nuclear portion; and as the outer layers are (on account of lower refractive index) not able wholly to neutralize the excess of this action, we can only ascribe the effect of the more convex nucleus to the less convex lens total by assuming the higher index of refraction. This substitution of a conventional convex lens with two known surfaces and a uniform index of refraction for the complex dioptric apparatus of the actual crystalline lens is one step in the process of working out a "schematic eye" which is the average dioptric equivalent of the normal emmetropic eye, and through which we are able to solve various problems in practical physiological optics. With the substitution of the equivalent or reduced crystalline lens we are able to consider the refraction of the eye as occurring at three surfaces,—the anterior surface of the cornea, the anterior surface of the lens, and the posterior surface of the lens. After the removal of the crystalline lens, as for cataract, there remains but a single refracting surface, the anterior surface of the cornea. This is also the condition of the so-called *reduced eye*, to be described later.

In such an aphakic eye, assuming the curvature of the cornea to be spherical, we have the problems of ocular refraction reduced to their simplest terms.

The Aphakic Eye.—The straight line F^1F^2 passing through the centre of curvature N of the corneal surface and through the centre of the surface C in Fig. 30 is the *primary* or *principal axis* of the dioptric system, or the *optic axis*. The point C where this axis pierces the refracting surface is called the *principal point*, and a plane HH passed through the principal point perpendicular to the axis is the *principal plane*.

Fig. 30.



In any consideration of the refraction of such an eye it is assumed that the bending of rays all takes place at this principal plane. A glance at the figure shows that this assumption is not strictly accurate, for the plane manifestly does not coincide throughout with the anterior surface of the cornea, where the bending really occurs. But for a small space at the centre of the cornea the principal plane and the corneal surface so nearly coincide that the assumption is accurate enough for all practical purposes, and our whole optical theory of lenses is based on such assumptions. To abandon such assumptions and attempt to work out a formula that would apply with perfect accuracy would be to make the subject infinitely more complex; and even then we should still be working with an assumed eye that would in some respects differ from every actual eye in existence.

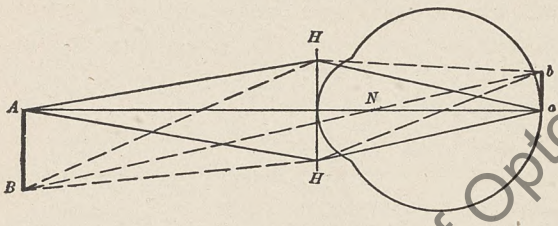
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Rays passing in the air parallel to the axis F^1F^2 and entering the eye are refracted (at the principal plane HH, it is assumed) towards a certain point F^2 on the axis. This point is called the *posterior* or *second principal focus.* The *anterior* or *first principal focus* is the point F^1 towards which would be refracted rays passing in the vitreous parallel to the principal axis (see broken lines on Fig. 30) and emerging from the eye. Conversely, rays coming from the second principal focus and passing into the air are rendered parallel to the axis, and rays coming from the first principal focus and entering the eye pass parallel in the vitreous. The distance F^1C from the first principal focus to the principal plane is the *first* or *anterior focal distance.* The distance CF^2 from the principal plane to the second principal focus is the *second* or *posterior focal distance.* These focal distances are directly proportional to the indexes of refraction of the media in which they are measured. With the index of air 1, and that of the cornea, aqueous, and vitreous 1.337,

$$F^1C : CF^2 :: 1 : 1.337.$$

The centre of curvature N of such an eye is also the *nodal point* of the eye. All rays coming towards it, or from it, pass through the surface of the cornea unrefracted because they are perpendicular to that surface. Each of these rays is the axial ray of a pencil coming to the eye from the point from which it emanates. Fig. 31 represents the eye with its principal plane, at which the refraction is assumed to occur, receiving rays from one point A on the primary axis which are converged to a, and rays from another point B outside of the primary axis, the ray BN passing through the nodal point and being met by the other rays from B at b. BN holds the same relation to the rays emanating from B as the primary axis holds to rays from A, and is called a *secondary axis.*

Fig. 31.



If we have the line AB and draw a line joining a and b, from each point of AB rays will enter the eye, to be converged to a corresponding point on ab; and one of these rays passing through the nodal point N, and therefore unrefracted, constitutes for each point of AB a secondary axis, and determines the direction in which each pencil of rays will converge. Each point of ab is then the *image* of a corresponding point of AB, and the whole line ab is the image of the whole line AB.

The relative *size of an image* depends on its relative distance from the nodal point; for in the triangles ABN and abN, the sides being parallel, the triangles are similar and the sides proportional. Thus,

$$AN : AB :: aN : ab.$$

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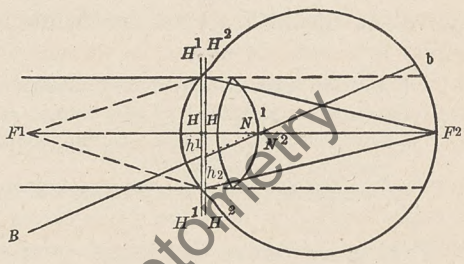
Having any three terms of this proportion, the fourth is readily found. For instance, having the size of an object and its distance from the nodal point of the eye, and knowing the distance of the nodal point N from the retina, we have:

$$\frac{\text{Size of object} \times \text{distance of retina from } N}{\text{distance of object from } N} = \text{size of image.} \qquad \text{(E)}$$

The relations of the nodal point to the position and size of images give it practical importance.

The Schematic Eye.—For the aphakic eye we could assume without important error that the refraction all took place in one principal plane. For the schematic eye, with its three refractive surfaces situated some distance apart, that assumption must be abandoned. We may, however, for such an eye, or for any number of spherical surfaces having the same principal axis,—having their centres of curvature in the same straight line,—assume with practical accuracy that the refraction of the lens system occurs in two planes, the position of which will depend on the relative position and lens-action of these different surfaces. These principal planes are separated by a certain interval, and there go with them two nodal points separated by the same interval. The relation of these planes and points in the schematic eye is shown in Fig. 32.

FIG. 32.



F^1F^2 is the *primary* or *principal* or *optic axis*,—the straight line in which are located the centres of curvatures of the three surfaces. H^1H^1, perpendicular to the optic axis, is the first or anterior principal plane, its intersection with the optic axis being the first principal point. H^2H^2, also perpendicular to the optic axis, is the second or posterior principal plane, and its intersection with that axis is the second principal point. F^1 is the first or anterior principal focus,—the focus for rays parallel in the vitreous,—and is situated the anterior focal distance in front of the first principal plane. F^2 is the second or posterior principal focus, situated the posterior focal distance behind the second principal plane. The relation of these focal distances is in general the same as the relation of the index of refraction of the first medium (in this case air) to the index of refraction of the last medium (in this case vitreous humor).

The first or anterior nodal point is N^1, and the second or posterior nodal point is N^2. A secondary axis Bb does not, for such a system, constitute a single straight line, but consists of two parts,—one, BN^1, a straight line extending from the source of the light towards the first nodal point N^1, until it reaches the first principal plane at h^1, and the other, h^2b, extending from h^2 in the second principal plane through the second nodal point, N^2.

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The points h^1 and h^2 are equally distant from the optic axis and in the same direction (that is, h^1h^2 is parallel to the optic axis), and h^2B is parallel to Bh^1. In general, all secondary axes pass before refraction towards the first nodal point, and after refraction through and from the second nodal point in a direction parallel to their first direction. Or, conversely, all rays passing towards the first nodal point or from the second nodal point continue parallel to their original direction, and are secondary axes. Between the principal planes the course of all rays is assumed parallel to the principal axis, whatever their direction in front of the first principal plane or beyond the second principal plane.

The following are means of the careful ophthalmometric measurements of many eyes:

	Millimetres.
Radius of curvature of cornea	7.829
Radius of curvature of anterior surface of lens, the ciliary muscle being relaxed	10.
Radius of curvature of posterior surface of lens	6.
Distance from summit of cornea to anterior pole of lens	3.6
Thickness of crystalline lens	3.6

The indexes of refraction as determined for the other media, and the equivalent calculated for the crystalline lens, are:

	Millimetres.
For cornea, aqueous humor, and vitreous humor	1.3365
Equivalent crystalline lens (Helmholtz's latest)	1.4371
Equivalent crystalline lens (Listing, adopted by Donders and formerly by Helmholtz)	1.4545
Equivalent crystalline lens (Aubert and Matthiessen)	1.4480

Taking the above dimensions, with the later index of Helmholtz for the equivalent crystalline lens, calculation gives for the schematic eye the following distances:

	Millimetres.
Summit of cornea to first principal point	1.7532
Summit of cornea to second principal point	2.1101
Summit of cornea to first nodal point	6.9685
Summit of cornea to second nodal point	7.3254
Distance between the principal planes equal the distance between the nodal points	0.3569
First nodal point in front of posterior pole of lens	0.2315
Second nodal point behind posterior pole of lens	0.1254
Anterior focal distance (measured from first principal plane)	15.4983
Posterior focal distance (measured from second principal plane)	20.7136
Anterior focus in front of summit of cornea	13.7451
Posterior focus behind summit of cornea	22.8237
Posterior nodal point to posterior focus	15.4983

If the eye be emmetropic, the retina is situated at the posterior focus, its distance from the anterior surface of the cornea is the antero-posterior axis of the eyeball, and the distance from the posterior nodal point to that

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focus is the distance of the retina, where images are formed, from the nodal point,—the distance which determines the size of the retinal image.

The Reduced Eye.—It will be observed that, among the values given for the schematic eye, the distance between the principal planes or the distance between the nodal points is a little over one-third of a millimetre, and also that this space is in various ways a space where nothing happens. It does not enter into the anterior or posterior focal distances or into conjugate focal distances. Since in it rays remain parallel to the axial ray, it does not affect the size of circles of diffusion. Neither does it affect the relative sizes of images, for these depend on the distance of the object from the anterior nodal point and the distance of the image or the retina from the posterior nodal point.

For most purposes of practical dioptrics we may therefore bring the two principal planes together, and the two nodal points likewise, by making the further assumption that the refraction of the standard schematic eye is represented by that of a *reduced eye* with but a single refractive surface, that of the cornea. The most important requirements regarding such an eye are that it shall closely correspond to the schematic eye in its focal distances and in the distance of its nodal point from the retina. To secure these it is necessary to assume for the cornea of the reduced eye either a greater curvature or a higher index of refraction than the natural cornea possesses.

Four such reduced eyes, differing in some respects from one another, have been proposed by Listing, Donders, Stammeshaus, and von Hasner, and are found referred to in the literature of the subject. Their respective dimensions, cardinal points, and focal distances are given below. It will be borne in mind that in such an eye the nodal point is at the centre of curvature, and its distance back of the cornea equals the radius of curvature; also that in such an eye, supposed to be emmetropic, the antero-posterior axis equals the posterior focal distance. The figures indicate distances in millimetres.

	Listing.	Donders.	Stammeshaus.	Von Hasner.
Radius of curvature of cornea . . .	5.077	5.	5.2152	7.5
Index of refraction	1.337	$1.33\frac{1}{3}$	1.3365	1.5
Anterior focal distance	15.036	15.	15.4983	15.
Posterior focal distance	20.113	20.	20.7135	22.5
Distance from nodal point to retina .	15.036	15.	15.4983	15.

On comparing these assumed optical equivalents of the human eye, it will be noted that the first three have adopted approximately the index of refraction of the cornea, with a much shortened radius of curvature. Von Hasner, however, has adopted a curvature approximating that of the average cornea, and a much higher index of refraction, one approaching that of ordinary optical glass. This gives a length of eyeball approximating the usual length of the eye, but an excessive posterior focal distance. It will be seen that the values decided on by Listing and Stammeshaus approximate very closely those of the schematic eye, while those of Donders and von Hasner are rougher approximations, which are very much easier to remem-

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ber and work with. As a chief value of the reduced eye is to enable one to solve quickly by mental calculation some of the problems that arise in practical work, the extreme simplicity of the latter eyes gives them the greater practical value.

Suppose, for instance, it is desired to find the height of the image formed on the retina by a man 1.8 metres high, 6 metres from the eye. By the formula (E) we have, reducing all to millimetres,

$$\frac{1800 \times 15}{6000} = 4.5.$$

Or suppose a certain scotoma causes blindness over a space 30 millimetres in diameter on a surface (the arc of a perimeter) 300 millimetres away,

$$\frac{30 \times 15}{300} = 1.5 \text{ millimetres},$$

the actual diameter of the scotoma.

Circumstances influencing the Positions of the Cardinal Points.—As has been indicated, the dimensions given are those for an assumed standard or average eye, from which any given eye will vary; and just what the variations are in a particular case can be ascertained only by careful opthalmometrical measurements of both the cornea and the crystalline lens, such as are practicable only for a comparatively few eyes in the well-equipped laboratory. In general, increased convexity of the surfaces will cause shortening of the focal distances; their comparative flattening will increase those distances. Absolute increase in the curvature of the cornea alone, or relative increase in its curvature as compared with the surfaces of the lens, or a more anterior position of the lens, will bring the principal and nodal points closer to the cornea. A greater depth of the lens, or its relatively greater curvature as compared with the cornea, will cause the principal and nodal points to fall deeper within the eye. The position of these points is also influenced by ametropia and the lenses used to correct it, as will be indicated in the account of these.

Emmetropia.—The discussion of the refraction of light within the eye is thus far complete, without taking any account of the position of the retina. Although the position of the retina with reference to the cardinal points of the eye, especially the posterior principal focus and the nodal point, is of the highest practical importance, the bending and course of the rays are in no way dependent on it.

The position of the retina with reference to the focus of the dioptric media is important, because the whole focussing apparatus exists to furnish the retina with assorted light, and the assorting of the light is complete only at the focus of the dioptric system. In front of this the rays of the same pencil still occupy a certain area and are intermingled with rays from other pencils, and beyond the focus they again spread out and intermingle. When the refracting surfaces of the eye are such that without effort of

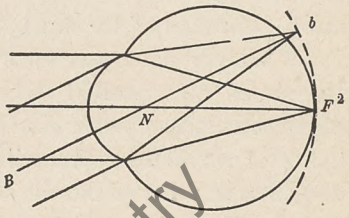
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the ciliary muscle they can bring rays of light parallel in the air to a perfect focus, and the retina is situated at that focus, the eye is said to be *emmetropic*. When the dioptric surfaces do not perfectly focus the light passing through them, or when they do so focus it but the retina is situated elsewhere, the eye is said to be *ametropic*. *Emmetropia* gives the eye certain advantages which will appear by contrast with the disadvantages of the various forms of *ametropia*. The various departures of the eye from emmetropia are called *errors* or *anomalies of refraction*.

It must be borne in mind, however, that in no eye is the whole retina so situated as to receive perfectly focussed rays that have been parallel in the air. We may more accurately define emmetropia to be the state of ocular refraction in which the part of the retina pierced by the optic axis, the region of the macula, receives perfectly focussed the rays which were parallel in the air.

That only a limited part of the retina can be so situated is illustrated by Fig. 33, which represents the reduced eye, to which is added an arc (the broken line) described with a radius NF^2 about the nodal point as a centre. Evidently it is the different points of this arc, and not of the retina, that are distant the posterior focal distance behind the cornea. Hence rays parallel to any secondary axis *Bb* will be focussed on this arc and behind the portion of the retina on which they fall.

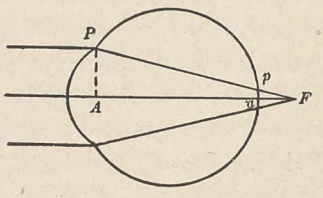
Fig. 33.



Thus, in the "emmetropic eye" only the central part of the retina is emmetropic, other parts being hyperopic. By a similar construction one may demonstrate that in hyperopic eyes the eccentric portions of the retina are more hyperopic than the central, and that in myopic eyes, aside from unequal bulging of the coats, the eccentric parts of the retina are less myopic, emmetropic, or even hyperopic. The refraction of an eye as it is commonly spoken of refers only to the position of the central part of the retina relative to the posterior principal focus.

Circles of Diffusion.—The pencil of rays entering the eye from any luminous point is limited by the outline of the pupil, approximately circular. If we suppose this circle to be situated in the second principal plane, the rays after leaving this plane occupy a cone with its base the pupil and its apex the focus towards which they tend. If at any point in front of or behind this focus the rays be intercepted by a plane parallel to the base, as by the retina, they will be found to occupy a circle the diameter of which is directly proportional to the diameter of the pupil and to the distance of the intercepting plane from the focus, and inversely proportional to the distance of the second principal plane from

Fig. 34.



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the focus. Thus, in Fig. 34 we have the similar triangles APF and apF, in which

$$AF : aF :: AP : ap,$$

or

$$ap = \frac{AP \times aF}{AF}.$$

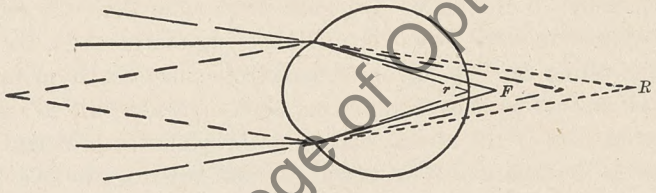
In calculating the size of diffusion circles formed on the retina, situated a known distance from the focus, one may, for all practical purposes, regard the plane of the pupil as coincident with the principal plane of Donders's reduced eye.

AMETROPIA.

Hyperopia.—Hyperopia is the term suggested by Helmholtz, and hypermetropia the one subsequently adopted by Donders, to designate that condition of the refraction of the eye in which, the accommodation being at rest, the retina intercepts the optic axis in front of the principal focus. The condition may be due to unusual flatness of the dioptric surfaces of the eye, in which case it is called *hyperopia of curvature;* or to the absence of the crystalline lens, *aphakic hyperopia;* but is most commonly due to undue shortness of the antero-posterior axis of the eyeball, *axial hyperopia.*

Whatever its cause, its optical and its clinical results are the same. Pencils of rays parallel before entering the eye are not focussed on the retina, but form upon it circles of diffusion; rays divergent before entering the eye form on the retina still larger circles of diffusion; and only rays convergent when they strike the surface of the cornea can be accurately focussed on the retina. These different conditions are illustrated in Fig. 35.

Fig. 35.



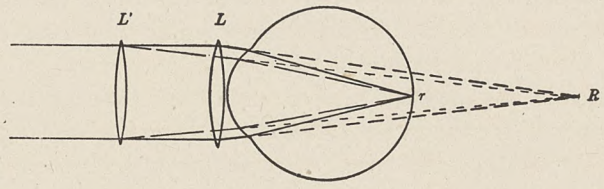
Only those rays having a certain degree of convergence, those converging towards a certain point back of the eye, will be focussed on the retina. Rays more convergent will be focussed in front of the retina, and those less convergent back of the retina. This point towards which the rays must be converging in order that the dioptric system of the eye can focus them upon the retina is a focus conjugate to the position of the retina. It is called the *far point* of the hyperopic eye. Rays coming from a point on the retina will, after emerging from the eye, diverge as though they had started from this focus. Thus, in Fig. 35, if rays converging towards R are focussed at r, rays from r will pass into the air divergent as if from R.

To secure the focussing of parallel rays upon the retina they must be

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rendered sufficiently convergent before entering the cornea, as by passing through a convex lens. The placing before the eye of a lens that will give parallel rays the proper convergence, and thus secure their focussing on the retina, is called *correcting the hyperopia*, and the lens which does it the *correcting lens*. It is convenient in practical work always to think of hyperopia as a deficiency of refracting power in the eye ; and the *degree* or *amount* of hyperopia is the refracting power of the infinitely thin convex lens which when placed at the surface of the cornea enables the eye to focus parallel rays on its retina. It is evident that a convex lens that will give parallel rays the proper convergence—turn them towards the focus conjugate to the retina—must be a lens with its principal focus at that point, or that any convex lens so placed before the eye that its principal focus falls at the conjugate to the retina will correct the hyperopia. Thus, in Fig. 36, if we

FIG. 36.



suppose the focus R to be three inches from the lens L placed before the eye, this lens would need to have a focal distance of three inches (or 13 D. of refracting power) to correct the hyperopia. But if another lens L' were used in a position one inch farther from the eye, it would need to have a focal distance of four inches (a refracting power of only 10 D.) to correct the hyperopia. If the convex correcting lens is to be worn a certain distance in front of the eye, it must have a certain strength ; nearer to the eye it needs to be stronger, farther from the eye it must be weaker.

In young persons hyperopia may be corrected by increased curvature of the crystalline lens, having the effect of a supplementary convex lens within the eye, as well as by the convex lens placed in front of the eye, and is commonly so corrected.

The *position of the second nodal point* is affected by hyperopia and its correction in a way that is of some practical importance. Hyperopia of curvature causes but little change in it, and may be disregarded. In axial hyperopia, the position of the nodal point remaining the same as in emmetropia with regard to the corneal surface, the shortening of the anteroposterior axis of the eyeball brings the retina by so much nearer to it, and proportionately decreases the size of the retinal images. In aphakia the nodal point comes to be the centre of curvature of the cornea, usually slightly farther back than the second nodal point of the reduced eye ; but the effect of this, taken by itself, is trifling.

The correction of the hyperopia by a convex lens placed before the eye produces an important change in the position of the nodal point, carrying

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it forward to an extent directly proportioned to the amount of the hyperopia corrected and the distance of the correcting lens before the eye. Of two lenses correcting a given amount of hyperopia, the weaker lens placed farther from the eye produces the greater effect on the position of the nodal point. In axial hyperopia the placing of a correcting lens at the anterior focus (about the distance in front of the eye that it is usually placed) will cause the nodal point to fall just the same distance in front of the retina that it does in the emmetropic eye, and will give retinal images of corresponding size. In hyperopia of curvature or aphakia the correcting lens brings the nodal point farther from the retina and gives larger retinal images. On account of the effect on the nodal point of the correcting lens placed at the anterior focus, it has been proposed to consider the strength of this lens the measure of the hyperopia; and in practical work and the reporting of cases the degree spoken of corresponds to this position of the lens rather than to one at the corneal surface. The correction of hyperopia by accommodation, and its effect on the region of accommodation, will be discussed under accommodation.

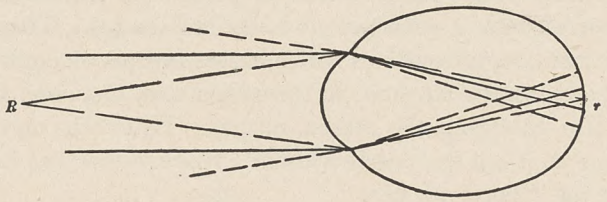
The change in the length of axis required to produce a certain degree of axial hyperopia is shown in the following table, and also, for purposes of comparison, the axial changes that cause similar degrees of myopia. The first column gives the degree of ametropia, the second the length of the axis in hyperopia, the third the length of the axis in myopia, the fourth the diminution of the axis in hyperopia, and the fifth the increase in the axis in myopia. Hyperopia of over 10 or 12 D. is rarely seen, aside from aphakia; while myopia upward of 20 D., almost always axial, is quite frequently encountered. A glance at the table indicates the enormously greater distortion of the eyeball in the latter condition. The figures of the first column indicate dioptres, those of the other columns millimetres.

Dioptres.	Hyperopia. Axis.	Myopia. Axis.	Hyperopia. Diminution.	Myopia. Increase.
0	22.824	22.824	. .	. .
1	22.51	23.14	.31	.32
2	22.20	23.48	.62	.66
3	21.90	23.83	.92	1.01
4	21.61	24.19	1.21	1.37
5	21.32	24.56	1.50	1.74
6	21.06	24.95	1.76	2.13
7	20.80	25.34	2.03	2.52
8	20.54	25.75	2.28	2.93
9	20.29	26.17	2.53	3.35
10	20.04	26.62	2.78	3.80
11	19.80	27.08	3.02	4.26
12	19.57	27.55	3.25	4.73
13	19.35	28.05	3.47	5.23
14	19.13	28.56	3.69	5.74
15	18.91	29.10	3.91	6.28
16	18.71	29.65	4.11	6.83
17	18.50	30.23	4.32	7.41
18	18.30	30.85	4.52	8.03
19	18.11	31.47	4.71	8.65
20	17.92	32.13	4.90	9.31

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Myopia is that condition of the refraction of the eye in which the principal focus falls in front of the retina. It may be due to excessive curvature of one or more of the dioptric surfaces, *myopia of curvature;* or to increase in the index of refraction of the nucleus of the lens, *index myopia;* but commonly it is caused by excessive length of the antero-posterior axis of the eyeball, *axial myopia.* In any case a pencil of rays, parallel in the air, on entering the eye is so refracted as to focus in the vitreous, and, diverging again from its focus, forms on the retina a circle of diffusion. Rays convergent before entering the eye are focussed still farther in front of the retina, and form upon it a correspondingly larger circle of diffusion. Only rays reaching the cornea with a certain degree of divergence can be accurately focussed upon the retina, rays more divergent or less divergent being focussed behind or in front of the retina. The rays coming from R in Fig. 37 have the proper degree of divergence to be

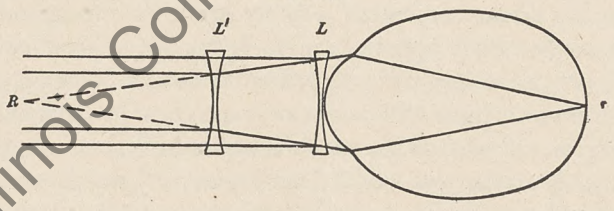
FIG. 37.



focussed on the retina at r. R and r have the relation of conjugate foci. Rays emanating from r, on passing out of the eye will be rendered so convergent as to be focussed at R, the focus conjugate to the position of the retina. R is the *far point* of the myopic eye.

To secure the focussing of parallel rays upon the retina of the myopic eye, they must be rendered divergent, as though from the far point R. This is accomplished by a concave lens which has its principal focus at the far point, and which is called a *correcting lens.* Evidently lenses of different strengths are equally capable of correcting a given amount of myopia if placed at their focal distances from R. Thus, in Fig. 38, if a lens L

FIG. 38.



placed at the anterior surface of the cornea is four inches from R, it must have a focal distance of four inches (refracting power of 10 D.) to correct the myopia; and another lens L' placed one inch in front of the cornea would be only three inches from R, and would require a focal distance of

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three inches (refracting power of 13 D.) to correct the same myopia. The nearer a concave lens is to the cornea the more myopia does it correct, or the weaker it can be to correct a given amount of myopia. Strictly speaking, the infinitely thin lens which corrects the myopia when placed at the surface of the cornea is the lens whose strength measures the amount of myopia. But in practice the lens which corrects it when placed in front of the eye in the ordinary position of the correcting lens is regarded as the measure of the amount. For the higher degrees of myopia it should always be indicated which is meant, for the difference between the two is important. Thus, in the case supposed for Fig. 38, strictly speaking, the amount is 10 D.; yet in practice it would be corrected by an 11 D. or 11.50 D. lens, and would be so recorded in the case-book or in reporting the case.

The *position of the second nodal point* with reference to the retina is thus affected by myopia and concave correcting lenses. The elongation of the antero-posterior axis of the eyeball in axial myopia carries the retina farther from the second nodal point than is its position in the emmetropic eye, causing a corresponding enlargement of retinal images. The increase of curvature in the dioptric surfaces which causes myopia of curvature brings the nodal point somewhat closer to the cornea and, therefore, farther from the retina, also enlarging the retinal images. Hence the myopic eye, for such distances as it can see clearly without a concave lens, has larger retinal images than the emmetropic eye.

A concave lens added in front of the dioptric system of the eye causes the second nodal point to be displaced farther from the cornea and nearer to the retina. The amount of such displacement increases directly with the strength of the concave lens and its distance in front of the cornea. If the correcting lens be placed at the anterior focus, its effect will be such that in axial myopia the nodal point will fall the same distance from the retina as in the emmetropic eye. In curvature myopia the effect of a correcting lens in front of the cornea is always to give a nodal point closer to the retina and a smaller retinal image than in emmetropia.

Astigmatism.—We have thus far assumed that the dioptric surfaces of the eye were small portions of spherical surfaces,—that they curved equally in all parts and in all directions. In reality, while they approach the spherical in form, they never exactly attain it throughout their extent. They more nearly approach in form an ellipsoid of two axes, and still more nearly an ellipsoid developed on three axes, because the tri-axial ellipsoid permits of those differences of curvature in different directions and in different portions of the surface which are to be observed in the dioptric surfaces of the eye. These variations of form give rise to varieties of curvature ametropia, some of which are of the highest practical importance.

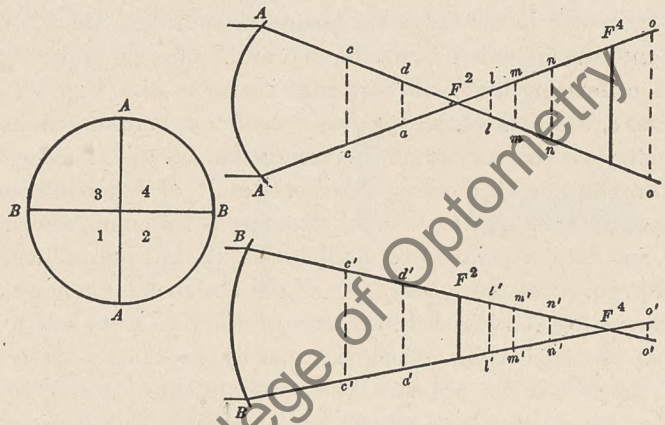
When the curvature of one or more of the dioptric surfaces of the eye is the same in different parts of the surface, but is different in different directions, in such a way that the direction in which it is most convex is

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perpendicular to the direction in which it is least convex, it gives rise to the form of ametropia known as *regular astigmatism*. The writer is accustomed to illustrate such a curvature by that of the edge of a watch, the curve of least convexity being in the plane parallel to the dial of the watch and the curve of greatest convexity in a plane perpendicular to the dial. Another common illustration is the convex surface of the bowl of a spoon. The dioptric surface which most constantly and markedly presents this anomaly of curvature is that of the cornea. It may, however, reside in either surface of the lens, or the same effect may be produced by obliquity of one or more of these surfaces to the entering pencil of rays.

When a pencil of rays enters the eye through a surface of the kind described, since the refraction of the rays is dependent on the curve of the surface, it will be greater in the direction of the curve with the shorter radius than in the direction of the curve with the longer radius, and the refraction at any particular point of the cornea may be regarded as made up of these two unequal factors. The changes occurring in a pencil of rays by reason of such refraction may be understood by supposing a case of astigmatism in which, according to the rule, the curve with the shorter radius is vertical and the curve with the longer radius is horizontal. In Fig. 39, let *ABAB*

FIG. 39.

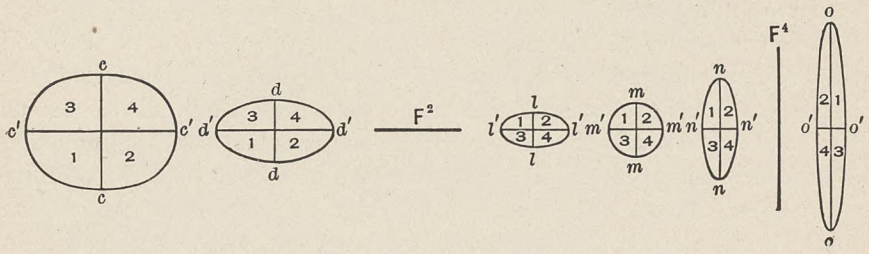


represent this cornea receiving a pencil of parallel rays, *AA* being a vertical and *BB* a horizontal section of it. On account of the greater curve in that direction, rays will be turned up and down more than they will be turned in from the sides; they will converge faster vertically than horizontally. Consequently, when at F^2, the posterior principal focus for the vertical curvature, the rays entering the lower half of the cornea have come up to the level of the central ray, and the rays entering the upper half of the cornea have come down to that level, they will still remain spread out the length of F^2 horizontally. Passing F^2, they begin to diverge again vertically, the rays that entered the lower half of the cornea spreading out above the central ray, and those that entered the upper half spreading out below the cen-

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tral ray; but from side to side they still converge towards the middle, until those entering the right half of the cornea have come over to the central ray, and those entering the left half have come over to the central ray at F^4, the posterior principal focus for the horizontal curvature. By this time the rays have diverged considerably up and down, and after passing F^4 they diverge laterally also. The form of the pencil of rays at different points—that is, the form of the diffusion areas to which it gives rise if intercepted—is shown in Fig. 40, in which sections of the pencil taken at *c*, *d*, F^2, *l*, *m*, *n*, F^4,

FIG. 40.



and *o* are represented. The lettering in the two figures corresponds throughout. In all of these areas the position of the rays that entered through the different quadrants is indicated by the same numbering, which serves to indicate the course of the rays as they pass backward: thus the rays indicated by 1 start in the lower left quadrant, continuing there to F^2, when they pass into the upper left quadrant, and at F^4 into the upper right quadrant. On comparing these different diffusion areas with Fig. 39, it will be noted that at *c*, while the pencil has grown smaller in both directions, the vertical diameter *cc* is shorter than the horizontal diameter *c'c'*, making the diffusion area an ellipse with the long axis horizontal; at *d* this difference is still more pronounced; at F^2 the vertical diameter is zero, and the rays are all collected, not into a point as by a spherical lens, but into a line called the *first* or *anterior focal line*. Back of F^2 the horizontal diameter continues to shorten with the continued convergence of the rays from side to side, but the vertical diameter begins to lengthen, and the rays that were in the lower quadrants are now in the upper. At a certain point *h* (nearer F^2 than F^4, because the rays intersect at a greater angle vertically than horizontally) the vertical and horizontal diameters become equal, and the diffusion area takes the form of a circle. Beyond this, the vertical diameter increasing while the horizontal still diminishes, the area becomes an ellipse with its long axis vertical, and it continues to become longer and narrower until the horizontal axis becomes zero, and we have at F^4 a vertical line, the *second* or *posterior focal line*. Here the rays that were in the right quadrants go over to the left, and those that were in the left quadrants cross to the right. From F^4 the rays diverge laterally as well as vertically, and at any point *o* give the diffusion area of an ellipse with its long axis vertical.

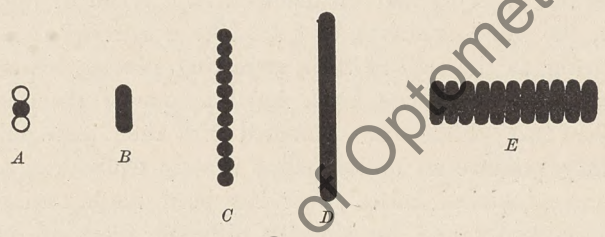
It is seen, then, that a dioptric system the seat of astigmatism cannot bring the rays from a single point together again at another point, but can

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only collect them into focal lines. These focal lines are perpendicular to one another, and are situated at different distances from the cornea, the distance of the horizontal line being determined by the vertical curvature and the position of the vertical line by the horizontal curvature. The interval $F^2\ F^4$ between these focal lines is called the *focal interval of Sturm*. The greater this interval the longer the focal lines, the shorter the interval the shorter the lines; and when (the curvatures becoming equal in the two directions) the focal lines come together, they merge in the single point to which the non-astigmatic dioptric system can bring rays that come from a single point. The direction of greatest curvature and the direction of least curvature are called the *principal meridians* of the astigmatic cornea or astigmatic eye, or the *meridians of astigmatism*.

The *appearance of lines to the astigmatic eye* depends on their direction relative to the meridians of astigmatism. A line consists of a succession of points, each of which makes its own impression on the retina, and the series of these impressions constitutes the impression of the line. In the non-astigmatic eye the light from one point of the line is focussed to one point within the eye, and if the retina be properly situated, each point of the line makes its distinct impression on the retina without overlapping neighboring points. In the astigmatic eye, however, the best that can be done with the rays from a single point is to bring them together into a focal line, which must overlap the impressions of points adjoining it in the direction of the line. This is illustrated in Fig. 41, in which *A* represents the impression

FIG. 41.



made by a point on the non-astigmatic eye, the points above and below it not confused with it; while *B*, the impression made on the retina of the astigmatic eye, so situated as to receive the vertical focal lines, overlaps and confuses the impressions of the points above and below it. The impression of a line in the non-astigmatic eye is represented at *C* as that of a succession of independent points. When in the astigmatic eye the line happens to run in the same direction as the focal line falling on the retina, the impression made by any one point of the line overlaps the impressions of adjoining points of the line, and not the space on either side of the line, so that the impression is, like *D*, that of a distinct line with shaded ends. When, however, the line looked at does not run in the direction of the focal line on the retina, this focal line overlaps not the line itself, but the space above and below it, giving the impression of a broad, indistinct band *E*. By the

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astigmatic eye lines are seen distinctly only when they run in the direction of the focal line falling on the retina.

Correction of Astigmatism. Cylindrical Lenses.—The correction of astigmatism consists in compensating the difference between the curvatures of the two principal meridians by an appropriate cylindrical lens, which will, if convex, add its effect to that of the less convex meridian and thus equal the refraction of the more convex meridian, or, if concave, will, by partly neutralizing the effect of the more convex, leave a remainder just equal to the effect of the less convex meridian. For the correction of a given case of astigmatism a cylindrical lens must be selected the refractive power of which equals the difference between the refractive powers of the principal meridians of the eye. It may be either convex or concave. If convex, its curve must be placed parallel to the less convex meridian of the eye, its axis parallel to the focal line the position of which the curve of that meridian determines. If concave, its curve must be in the direction of the more convex meridian of the cornea, its axis parallel to the focal line whose position is determined by that curve.

Combinations of Cylindrical Lenses.—It should be borne in mind that any case of regular astigmatism can be corrected by a single cylindrical lens (either convex or concave) of the proper strength and properly placed. If two cylindrical lenses are employed before the same eye, with their axes perpendicular the one to the other, they act, when of the same kind (both convex or both concave), like a cylindrical lens with a refractive power equal to the difference between the two, combined with a spherical lens with a refractive power equal to that of the weaker. When of opposite kinds (one convex, the other concave), they act like a cylindrical lens equal in refractive power to the sum of their refracting powers, combined with a spherical lens of the opposite kind, equal to one of them in refractive power. When two cylinders are combined with their axes oblique one to the other, they produce an optical effect exactly equivalent to that of a certain sphero-cylindrical lens. This has been mathematically demonstrated, independently and by slightly different methods, by Donders, Hoorweg, Oliver and Hay, Jackson, Prentice, and Weiland. The author's demonstration with a practical method of ascertaining the sphero-cylindrical equivalent in any given case is contained in the *Transactions of the American Ophthalmological Society*, 1886, p. 268. A very ingenious instrument for the purpose of finding this and other equivalents is described by Weiland in the *Archives of Ophthalmology*, 1893, p. 433.

Effect of Astigmatism and Cylindrical Lenses on Nodal Points and Images.—Since the positions of the principal points and nodal points of the eye depend on the curvature of its dioptric surfaces, the greater curvature of these surfaces in one meridian than in another causes such points to lie at different depths in the eye for the different meridians. The greatest interval between the corresponding points of different meridians is produced by differences of curvature in the cornea, the common seat of this anomaly of curvature.

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In general, the meridian having the shorter radius of curvature—the greater refractive power—has its principal and nodal points near the cornea and its posterior nodal point farthest from the retina. On this account images in this meridian are larger, as compared with the size and distance of the object, than images formed in the other principal meridian. Thus, a square held with its sides parallel to the principal meridians of such an eye gives a retinal image rectangular in form, with the sides parallel to the meridian of greatest curvature slightly longer than the other sides. A circle gives an ellipse with its long axis parallel to the meridian of greatest curvature. Such a distortion of the retinal images causes the images of lines not parallel to principal meridians, as the diagonals of the square referred to above, to depart somewhat from parallelism to the lines themselves. This twisting of the image may be in different directions in the two eyes, leading to a lack of perfect correspondence of the retinal images in the two eyes. It must be borne in mind, however, that this twisting is comparatively slight, even for lines farthest removed from the directions of the principal meridians, and that such lines can never by the uncorrected astigmatic eye be seen with perfect clearness.

The correction of astigmatism by a cylindrical lens placed in front of the cornea necessarily affects the position of the nodal point in the meridian parallel to the curve (perpendicular to the axis) of the lens. A convex lens brings the nodal point forward, a concave lens carries it back from the cornea. This displacement varies with the strength of the correcting lens and its distance from the cornea, but it is always greater than the displacement caused by the astigmatism corrected. And being suddenly acquired instead of congenital or slowly developed, and involving lines now clearly focussed on the retina, the distortion it causes in the retinal images is generally noticeable and annoying, until the visual function has adapted itself to its new conditions.

Aberration.—The dioptric system of the eye is not exempt from the optical defect of spherical lenses, spherical aberration, although this is partly corrected by the diminished index of refraction towards the periphery of the lens and the form of the corneal surface. The surface of the cornea departs most notably from a spherical form, in that the periphery is considerably less curved than the centre. The crystalline lens, on the other hand, is much more convex near its periphery than at its centre. In the large majority of eyes the increased curvature of the lens predominates over the flattening of the cornea at the periphery of the pupil, so that in this portion the refraction of the eye is more myopic or less hyperopic than at the centre. In some eyes, however, the opposite is the case. (See article on Skiascopy.)

Chromatic aberration, or the separation of colors by reason of the different refrangibility of light of different colors, although fairly corrected for lens surfaces of such strong curvature, occurs to some extent in the eye. It may be demonstrated by looking in a darkened room at a point of light,

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through glass that intercepts the middle portion of the spectrum, permitting only the extreme rays—the red and blue or violet—to pass. With the focus slightly in front of the retina (myopia), there will be seen a red centre surrounded by a blue diffusion circle, and with the focus slightly back of the retina (hyperopia), a blue centre with a red diffusion circle about it. With astigmatism, one may in this experiment get the anterior focal line for red and the posterior focal line for blue both on the retina at the same time, forming a cross, with one line (the horizontal in astigmatism with the rule) red and the other blue.

Irregular Astigmatism.—Optical theory can deal only with the dioptrics of regular surfaces, regular astigmatism and aberration being anomalies dependent on such surfaces. But in the eye the surfaces developed by the processes of nutrition always lack something of perfect regularity, so that their action varies from perfect focussing in ways peculiar to the individual eye. This may be by unequal curves in different directions, as when the greatest and least curvatures are not perpendicular to each other, and the error, therefore, cannot be entirely corrected by cylindrical lenses; or it may be from unequal curves in different parts of the surface, as in the cornea after interstitial keratitis or phlyctenular disease; or it may be due to irregularities in the index of refraction, as in the crystalline lens before it becomes opaque. All errors of refraction from such causes are grouped under the head of irregular astigmatism. They cannot be corrected, except that the diffusion of light caused by them on the retina may be reduced to the minimum by narrowing the pupil or placing an opaque disk with a narrow opening before the eye,—*stenopaic spectacles.*

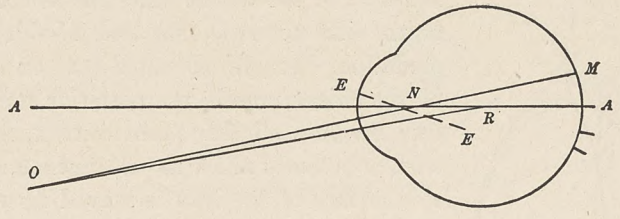
The Visual Zone.—In the vicinity of the visual axis regular astigmatism is, as a rule, the least; aberration is in most eyes well corrected, and irregular astigmatism very slight, so that the light entering through this part of the dioptric surfaces and media may be very perfectly focussed on the retina. This part I have called the *visual zone.* The essential thing about it is to remember that it does not include the whole of the dioptric surfaces of the eye, but is always surrounded by a region not capable of accurately focussing light, which may be called the *extra-visual zone.* The extent of the visual zone varies greatly in different eyes. In some its boundary is exposed only by considerable dilatation of the pupil, in others the extra-visual zone encroaches on the pupil even when contracted by strong light and with accommodation. The visual zone alone affords distinct vision. The extra-visual zone aids by the admission of more light when, on account of the feeble illumination, vision would be at best imperfect. Its imperfections are illustrated by the comparatively poor vision obtained by optical iridectomy or through the margin of a dislocated crystalline lens.

Centring of the Dioptric Surfaces.—It was assumed for the schematic eye that the dioptric surfaces constituted a centred system; but in reality they do not, and if we take as the optic axis the straight line passing through the centre of the corneal surface,—the centre of rotation of the eye-

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ball and its posterior pole,—it will generally be found that the centres of curvature for the different dioptric surfaces do not lie on this line, but depart from it in different directions and to various distances. It will also be found that this axis does not cut the retina at the fovea centralis. It is therefore necessary to recognize certain other lines and their relations. These are shown in Fig. 42, with their divergence exaggerated. *AA* is the optic axis,

FIG. 42.



on which *N* is the nodal point and *R* the *centre of rotation*, situated six millimetres behind the nodal point and nine millimetres in front of the retina. *O* is the object looked at, *M* the centre of the macula, and *OM* the *visual line*. *EE* is the long axis of the ellipsoidal anterior surface of the cornea, and *OR* is the *line of fixation* from the centre of rotation to the object. The angle between the axis of the corneal ellipse *EE* and the visual line *OM* is called the *angle alpha*, α; and the angle between the optic axis *AA* and the line of fixation *OM* is called the *angle gamma*, γ.

The angle gamma averages 5°, but varies in different eyes, being usually greater in hyperopia—as much as 10°—and less in myopia, or even negative, the optic axis piercing the retina to the temporal side of the macula. The angle alpha is usually slight, but may be larger than the angle gamma. These angles are of practical importance in connection with anomalies of the motor apparatus.

ACCOMMODATION.

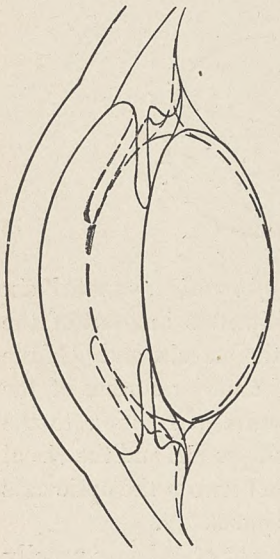
For any given dioptric system, rays, to be focussed at a certain point, must have a certain divergence or convergence; they must be diverging from or converging towards a certain other point, its conjugate. But to the eye come rays varying from extreme convergence to parallelism. It needs to focus on a fixed point—the centre of the retina—rays coming from objects at various distances. This it can do only by changes in its dioptric system. We have so far discussed this system as a fixed system. Its focussing power as a fixed system, compared with the position of the retina, is called its *refraction*. The power to vary its dioptric action to adapt it to focus on the retina rays coming from different distances is called the *power of accommodation*.

The accommodation of the eye is accomplished by change of shape in the crystalline lens under the influence of muscular action on the part of the ciliary muscle. The crystalline lens in early life is extremely flexible and elastic, and, stripped of its capsule, almost globular in shape. In the

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living eye, under the elastic tension of its capsule it is considerably flattened. This tension of the capsule is greatest and the lens flattest when the ciliary muscle is relaxed. Contraction of the ciliary muscle takes the tension of the capsule off the lens, which then, in proportion to its elasticity, becomes more convex. These changes are illustrated by Fig. 43, the continuous lines showing the outlines of the cornea, iris, ciliary region, and lens when the eye is at rest, and the dotted lines the altered outlines of the ciliary muscle, lens, and iris during accommodation. It will be noted that on contraction of the ciliary muscle the posterior surface of the lens becomes slightly more convex, the anterior surface becomes much more convex, and the anterior surface of the lens is moved forward, pushing the iris with it. Optically, the effect is chiefly that of the addition of a convex meniscus to the anterior surface of the crystalline, and its amount is measured by the strength of a convex lens which placed at the surface of the cornea would produce the same optical effect.

FIG. 43.



With differing degrees of contraction of the ciliary muscle, different degrees of increased convexity and increased refractive power are obtained. When the muscle is exerted to the utmost, the greatest increase of convexity possible to that eye is produced, and the change of refractive power it causes is the *total accommodation*. With extreme exertion of the ciliary muscle in children, the anterior surface of the crystalline lens becomes about as convex as the posterior surface, each having a radius of curvature of five millimetres or a little over; the lens becomes more than four millimetres thick, and its anterior pole but little over three millimetres behind the anterior surface of the cornea.

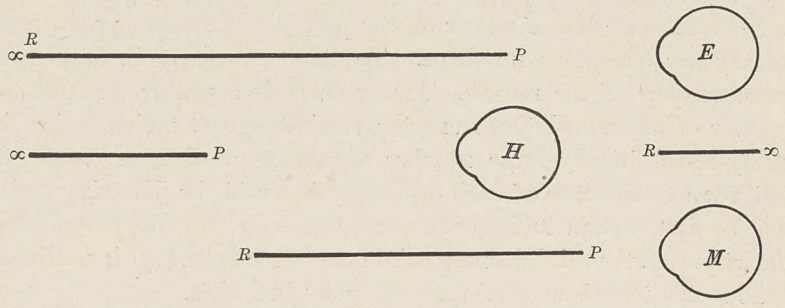
With variations of accommodation the eye is adapted to rays of different degrees of divergence, coming from various distances. When the total accommodation is brought into play, it is adapted for the most divergent rays that can be brought to a focus on the retina, rays coming from the nearest point to the eye from which rays can be focussed on the retina. This point is called the *near point* of distinct vision, or *punctum proximum*. When the ciliary muscle is relaxed, and the lens as flat as it can become, the eye is adapted for the least divergent rays that it can focus on the retina, and this point is called the *far point* of distinct vision, or *punctum remotum*.

The Region of Accommodation.—The far point is a focus conjugate to the retina when the accommodation is in abeyance, the one referred to in discussing hyperopia and myopia. The near point is the focus conjugate to the retina with the total accommodation exerted. By appropriate effort of the ciliary muscle, any intermediate point may be made conjugate to the

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retina and rays from it focussed on the retina. This intermediate space in which distinct vision is possible is the *region of accommodation.* The location of this region varies with the refraction of the eye, as is illustrated in Fig. 44, in which the heavy line indicates the region of accommodation,

FIG. 44.



R being the far point and *P* the near point. The upper diagram represents emmetropia, with the region starting at an infinite distance, where the far point of the emmetropic eye is situated, and extending to the near point, situated at the focal distance of a lens equal to the total accommodation in front of the eye. The middle diagram represents hyperopia, with the far point behind the eye, towards which the rays must converge to be focussed on the retina without accommodation. Thence the region of accommodation stretches back to an infinite distance, a sort of negative or virtual region of accommodation quite useless to its possessor, except that it represents the correction of the hyperopia that must be accomplished before distinct vision can begin, even at a distance. Beginning again in front, the region extends from an infinite distance to the near point, which is situated in front of the eye at the focal distance of a lens equal to the total accommodation minus the hyperopia. The lower diagram represents myopia, in which the region of accommodation starts at the far point in front of the eye, at the focal distance of the myopia, and extends to the near point at the focal distance of a lens equal to the myopia plus the accommodation. It should be noticed that the emmetropic eye has the most extended region of useful accommodation.

Accommodation in Astigmatism.—Since in astigmatism the focal lines are separated by a certain interval, but one of them can fall on the retina at one time. The state of the eye as to accommodation may, however, determine which shall fall on the retina, or may by rapid variation cause first one and then the other to fall on the retina in quick succession. So that in both directions lines may be seen distinctly at so brief an interval as to allow their combination into a distinct mental image. In this way astigmatism of low degree may not prevent distinct vision. It has been supposed that sometimes an unequal contraction of different parts of the ciliary muscle caused unequal increase of convexity in different meridians of the lens, and thus effected a true correction of astigmatism. But this is not proved. The cases supposed to illustrate it have not been observed with

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sufficient care to exclude error from the influence of conditions that might be present in the extra-visual zone.

Loss of Accommodation with Age: Presbyopia.—The change effected in the shape of the crystalline lens by the contraction of the ciliary muscle depends both on the power of the muscle and on the elasticity of the lens. From infancy there is a progressive increase in the rigidity of the lens, so that the same exertion of power on the part of the muscle produces progressively less change in its shape. To this is added late in life weakness or even atrophy of the muscle. Hence there is a progressive decline in the power of accommodation from the earliest age at which it has been carefully tested in any large number of persons until it is entirely lost. About the average rate of such decline is shown in the following table, in which the first column indicates the age, the second the dioptres of accommodative power, the third the near point for an emmetropic eye in millimetres, and the fourth the distance of the same point in inches.

Age.	Dioptres.	Millimetres.	Inches.	Age.	Dioptres.	Millimetres.	Inches.
10	14	71	2.81	45	3.5	286	11.25
15	12	83	3.28	50	2.5	400	15.75
20	10	100	3.94	55	1.5	667	26.25
25	8.5	118	4.63	60	.75	1333	52.49
30	7	143	5.63	65	.25	4000	157.48
35	5.5	182	7.16	70	0.	∞	∞
40	4.5	222	8.75				

The above table gives the total accommodation and the near point obtained by the maximum exertion of which the ciliary muscle is capable. Such exertion can be put forth for only a short time, and cannot be sustained for any continuous work. For continuous work only a fraction of the total accommodation is available. What this fraction is varies with different persons and at different ages. On the average, about one-half the total accommodation can be used at the age of thirty and about two-thirds of it after forty-five. When this fraction is no longer sufficient to give clear vision for the work required of the eyes, the failure of accommodation by age has progressed so far as to be a source of annoyance, pain, and danger to the eye, and is called *presbyopia*.

The advent of presbyopia will be earlier where a certain fixed portion of the accommodation is consumed in correcting hyperopia; but it will be later if myopia renders less accommodation necessary for near work, and when the myopia is sufficient to permit the doing of near work without any use of accommodation, presbyopia will not occur.

The effect of accommodation on the cardinal points of the eye is comparatively slight, since the change is mainly in the anterior surface of the lens. The principal points retreat from the cornea, but the nodal points slightly approach it. This places the posterior nodal point farther in front of the retina, and causes some enlargement of retinal images. Such enlargement is, however, much less than that produced by a convex lens placed in front of the cornea, which would equally alter the refractive power.

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THE PERCEPTION OF LIGHT.

BY J. McKEEN CATTELL, M.A., PH.D.,
Professor of Experimental Psychology, Columbia College, New York.

EXACT science consists of measurements and the relations of quantities. Physiology and psychology are far from this goal, but every movement should be in its direction. We may, therefore, with advantage follow in the path of physical science, and apply to the perception of light the three units required for measuring space, time, and energy. The field of vision, the acuity of vision, binocular vision, and other subjects related to the perception of space are reviewed elsewhere in this work. We have, consequently, in this place only to consider the measurement of intensity and of time.[1]

PART I.—INTENSITY.

I.—THE THRESHOLD.

Lights, sounds, and other physical stimuli may be so faint that they cannot be perceived. The intensity of the stimulus which just calls forth a sensation has been aptly called *the threshold*. The fact of the threshold may be partly due to inertia of the sense organs and dispersion in the paths of conduction, which might prevent the motion from arriving at those parts of the brain immediately concerned with consciousness. But the stimulation may, indeed, be carried on to the brain and be given in consciousness, but so faintly that under ordinary circumstances it escapes attention. In such a case we have to do with subconscious mental processes, —changes in consciousness which are not noticed, but which yet affect the course of mental life.

[1] The most important general works on the perception of light are the following:

Purkinje, J. E., Beobachtungen und Versuche zur Physiologie der Sinne, Part i., Prag, 1823; Part ii., Berlin, 1825.

Helmholtz, H. v., Handbuch der physiologischen Optik, Leipzig, 1867. A second revised edition is now (1895) in course of publication.

Aubert, Hermann, Physiologie der Netzhaut, Breslau, 1865.

Aubert, Grundzüge der physiologischen Optik, Leipzig, 1876. Reprinted from the Handbuch der gesammten Augenheilkunde, edited by A. Graefe and Th. Saemisch.

Fick, A., Die Lehre von der Lichtempfindung, in vol. iii. of Hermann's Handbuch der Physiologie, Leipzig, 1879.

Rood, Ogden N., Modern Chromatics, New York, 1879.

Wundt, W., Grundzüge der physiologischen Psychologie, 4th ed., Leipzig, 1893.

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In the case of vision we cannot obtain complete absence of physical light, nor can we avoid the idio-retinal light; the threshold is, therefore, the least light which can be distinguished in the field of vision when it is made as dark as possible. Aubert,[1] by observing the temperature at which metals begin to glow, estimated the just visible light at $\frac{1}{300}$ of that of the full moon reflected from white paper. König and Brodhun[2] have made more exact measurements. As unit of intensity they used the light of melting platinum reflected from a surface covered with magnesium oxide. The area of the platinum was 0.1 centimetre square, and it was at a distance of one metre from the reflecting surface, which was seen through the aperture of a diaphragm one millimetre square. The threshold for white light was about 0.0007 of this unit, and for colored lights varied between 0.11 (red, $\lambda = 670\ \mu\mu$) and 0.00012 (violet, $\lambda = 430\ \mu\mu$). The threshold for color has also been determined by Abney[3] and by Ferry.[4] Langley[5] has recently made a further advance in our knowledge of the subject by determining the actual energy (as heat) of the light which just excites a sensation. He determined the amount of light required to read the figures of a table of logarithms with the several colors. The energy (expressed as heat) was $\frac{1}{50000000}$ calorie, and only a small part of this energy would affect the retina. Langley calculates that in the case of one observer, and for green light, only the reciprocal of 310,000,000 ergs was required to call forth a sensation of light. Expressed in terms of horse-power, this would be 0.00000000000000000075 horse-power. The relative sensitiveness of the eyes of four observers for a constant amount of energy of varying wave-length is shown in the accompanying curves (Fig. 1) which the writer has drawn from Langley's table. Along the base-line are the colors together with the wave-length in micro-millimetres and Fraunhofer's lines. The relative sensitiveness for the different colors and the four observers is shown by the height of the curve above the base-line.

These curves show that the sensitiveness of one eye may be ten times as great as that of another, although the color-vision of both would be regarded as normal. Such a difference in the sharpness of hearing would be detected by the ordinary tests of the clinic, whereas it would escape the methods of the ophthalmologist. For three of the observers a given amount of energy produces the greatest effect in blue-green, and for one (Langley) in yellow-green. Langley notes that the younger observers were relatively more sensitive to the more refrangible rays. And the

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[1] Loc. cit.

[2] Experimentelle Untersuchungen über die psychophysische Fundamentalformel in Bezug auf den Gesichtssinn, Sitzungsber. d. Akad. d. Wiss. zu Berlin, 1889, ii. 641–644, June 27, 1889.

[3] Colour Measurement and Mixture, London and New York, 1891.

[4] Persistence of Vision, Am. Jour. of Sci., Ser. 3, xliv. 192–207, September, 1892.

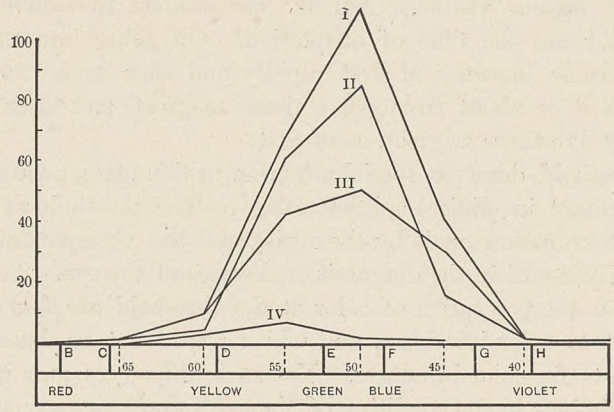
[5] Energy and Vision, Am. Jour. of Sci., Ser. 3, xxxvi. 359–379, 1888; also Mem. Am. Nat. Acad. Sci., vol. v., 1888.

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same observation has been made by Ferry,[1] independently and in experiments of a different sort. If this be the case, it will have an important bearing on theories of color-vision and development of the eye. The range of color-vision certainly requires investigation. It seems not unlikely that with increasing age the eye, like the ear, may lose the power of perceiving the quicker vibrations.

In these cases only light was seen, while the color could not be recognized. It is a common experience (as in twilight) that we can distinguish

FIG. 1.



lights and shapes when we cannot distinguish colors. Charpentier[2] found the threshold for red to be about twice as great as that for light without regard to color, and eighty times as great for violet as for red. The fact that all colors appear gray when the intensity is small and white when it is very great does not seem to be accounted for in a satisfactory manner by the Young-Helmholtz theory of color-vision. There seems to be no reason why a color which works chiefly on one sort of fibres or cells when of moderate intensity should affect the three sorts equally when faint or intense. This is one of a number of facts which make it necessary to assume that the visual mechanism is sensitive to gray and white independently of color. It seems natural that in the course of evolution the organism should have become sensitive to changes of light and darkness before the visual mechanism became fitted to perceive differences in color.

The threshold becomes greater as the area of stimulation is made smaller and as the time of stimulation is made less. The threshold is smaller for moving objects. Thus, if the eyelids be closed and the hand held between them and the sky, the hand can be seen when it is moved,

[1] Loc. cit.

[2] La perception des couleurs et la perception des formes, Compt. rend. de l'Acad. des Sciences, xcvi. 858–860, 1880; La perception des couleurs et la perception des différences de clarté, Compt. rend., xcvi. 1079–1081, 1883; Nouvelles recherches analytiques sur les fonctions visuelles, Arch. d'Ophthal., iv. 291–323, 1884.

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but not otherwise. So, also, we can see a moving object farther away from the fovea centralis than an object at rest. It is a general psychological law that we perceive changes rather than constant conditions. Nor are changes noticed which are very gradual. If the temperature of a plate on which a frog is sitting be raised very gradually, it will not move away, but will be burned up. Modern psychology has to a considerable extent confirmed the principle of Hobbes, "*Semper idem sentire ac non sentire ad idem revertunt.*"

The light which can just be seen varies with the sensitiveness of the retina and the size of the pupil. We all know that on first going into the dark we may be able to see nothing, whereas in a few minutes objects may become visible. Aubert[1] has studied the relation between the threshold and the time of adaptation. On going into a dark room the sensitiveness increases at first rapidly and then more slowly; after ten minutes it is about twenty-five times as great, and after two hours about thirty-five times as great, as at first.

The threshold deserves special attention in this place, owing to its possible importance in clinical ophthalmology. The threshold of hearing is the first determination made by the aurist, and the corresponding test may prove equally useful in the diagnosis of diseases of the eye. For example, variations in the perception of color at the threshold are found which do not amount to color-blindness, and which would not be detected by the ordinary tests for color-blindness. Yet such differences may indicate important variations in the condition of the eye and of the nervous system.

II.—THE PERCEPTION OF SMALL DIFFERENCES.

As a light may be so faint that it cannot be noticed, so the difference between two lights may be so small that no difference can be distinguished. Thus, the stars cannot be seen in the daytime. The light of the stars is not less than at night, but the difference between their light and the light of the sky is so small that no difference can be perceived. The least difference which can be noticed is an important physiological constant. It can be determined with greater ease than the just noticeable light, and, being a delicate test of the condition of the eye, will prove useful in diagnosis, serving to indicate small changes in progression or recovery.

Bouguer[2] was the first to measure the just noticeable difference. He found that a shadow could be distinguished from its background when the difference in the two lights was about one sixty-fourth. This method is illustrated in Fig. 2.

The white screen SS' is illumined by the candle at L. A second candle of the same sort, l, is placed at a greater distance from the screen. It will

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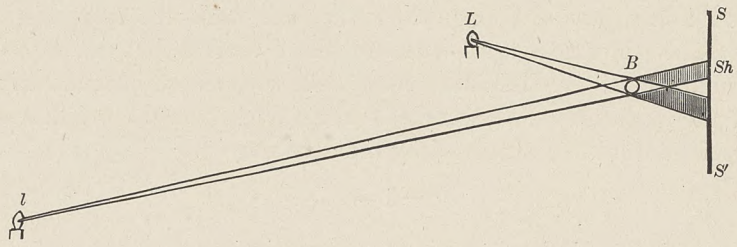
[1] Loc. cit.

[2] Essai d'optique, sur la gradation de la lumière, Paris, 1729; Traité d'optique sur la gradation de la lumière, Paris, 1760; Opus conversum in Latinum a Joachimo Richtenburg, Vindobonæ, 1762.

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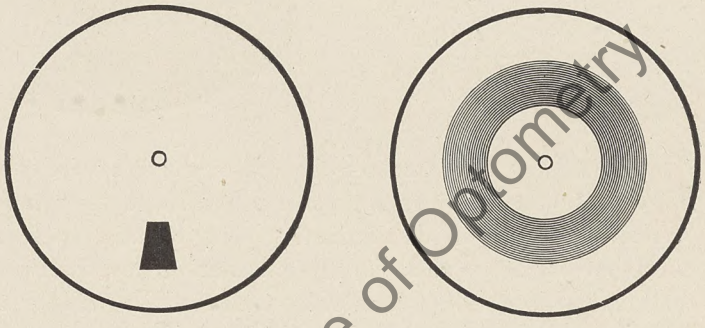
cast a shadow of the bar *B* at *Sh*, but when the candle is removed to a sufficient distance the shadow cannot be distinguished from the background. When *L* was (say) one foot distant and *l* eight feet distant, the shadow could not be seen, according to Bouguer, and, the illumination varying inversely as the square of the distance, the just noticeable difference was

FIG. 2.



about one sixty-fourth. With a brighter light the relation was not altered. The same or analogous methods have been used by Lambert,[1] Arago,[2] Rumford,[3] Volkmann,[4] Aubert,[5] and Cammerer.[6] Of these researches that by Aubert seems to be the most valuable. He altered the intensity of illumination, and found that with the brightest light, which was equal to

FIG. 3.



seven hundred and ten times the light of a candle at a distance of two metres from the illumined surface, the just noticeable difference was $\frac{1}{164}$, whereas with the faintest light, which was $\frac{1}{2731}$ of the candle, the just noticeable difference was one-third.

[1] Photometria, sive de mensura et gradibus luminis, colorum et umbræ, Augustæ Vindelicorum, 1760.

[2] Astronomie populaire, i. 192–194, Paris and Leipzig, 1854.

[3] An Account of a Method of Measuring the Comparative Intensities of the Light emitted by Luminous Bodies, Trans. of the Roy. Soc. London, lxxxiv. 67–106, 1794.

[4] Physiologische Untersuchungen im Gebiete der Optik, erstes Heft, Leipzig, 1863.

[5] Loc. cit.

[6] Zehender's Klinische Monatsblätter für Augenheilkunde, Jahrg. xv., 56 ff.

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Owing to the variation in the intensity and outline of the shadow due to flickering of the flames, and also for other reasons, such as the difficulty of avoiding diffused light, the just noticeable difference cannot be exactly determined by this method. Masson[1] used for the purpose revolving disks. On these blackened sectors may be painted, as shown in *A*, Fig. 3. When the disks are rapidly revolved, the blackened sector fuses with the white surface, making a gray ring, as shown in *B*. Masson found that the ring could only just be distinguished when the black was about $\frac{1}{100}$ of the circle. This difference varied with different observers, but not with different illuminations. v. Helmholtz used disks such as are illustrated in Fig. 4. If the brightness of the whole be taken as 1, then the brightness b of a gray circle would be expressed by the equation

$$b = 1 - \frac{d}{2r\pi},$$

in which d is the width of the line and r its distance from the centre of the

Fig. 4.

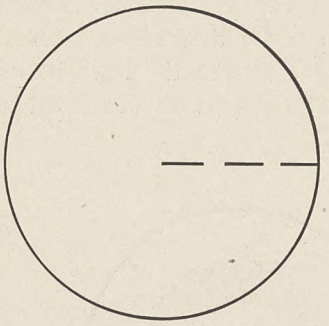
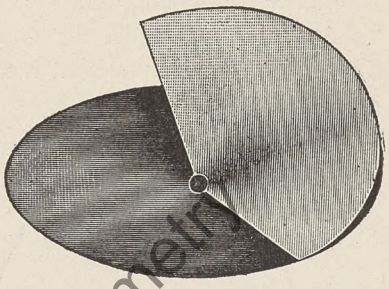


Fig. 5.



circle. By determining how far from the centre the gray circles are visible, v. Helmholtz found the just noticeable difference to vary from $\frac{1}{167}$ to $\frac{1}{117}$, the relative accuracy of discrimination being greatest in a moderate light. v. Helmholtz states that the rate of rotation was barely sufficient to cause fusion, and he does not seem to have allowed for the light reflected from the black nor for the length of line which would make the gray circle not uniform. Kraepelin[2] used similar disks in a more careful manner, and altered the intensity of the light by means of smoked glasses. He found the just noticeable difference to be about $\frac{1}{122}$ with the strongest light, and $\frac{1}{100}$ with the weakest. Aubert[3] used rotating disks of a different sort. Following Maxwell, he made black and white wheels with a slit as a radius, and pasted narrow white sectors on the black wheels. The wheels may be placed on the rotating machine so as to overlap, as in Fig. 5, and may be

[1] Études de photométrie électrique, Ann. de Chim. et de Phys., Sér. 3, xiv. 129–195, 1845; also Pogg. Ann. d. Phys. u. Chem., lxiii. 158-165, 1844.

[2] Zur Frage der Gültigkeit des Weber'schen Gesetzes bei Lichtempfindungen, Philos. Stud., ii. 306–326, 651–654, 1885.

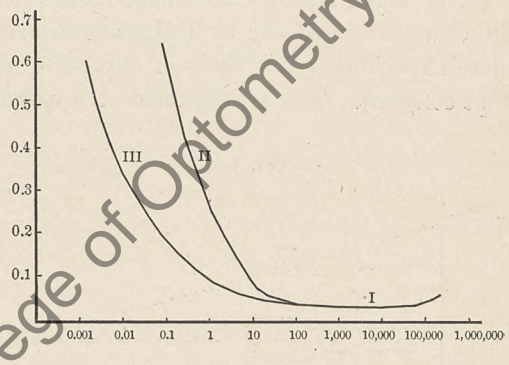
[3] Loc. cit.

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shifted so as to show more or less of the black. By increasing the amount of black until the gray could be just seen, Aubert found the just noticeable difference to vary from $\frac{1}{102}$ to $\frac{1}{186}$ of the light, being smallest when the light was from a clear sky, and larger when the sky was clouded or when the disks were illumined by direct sunlight. Schirmer[1] has recently made experiments with revolving disks, combining the methods of v. Helmholtz[2] and Aubert, and paying especial attention to adaptation. He finds the just noticeable difference (about $\frac{1}{217}$) to remain the same when the intensity is varied from one to one thousand metre-candles, and thinks the variations of other observers are due to the lack of proper adaptation, and that the relative constancy of the just noticeable difference may be explained by physiological conditions of adaptation. Revolving disks as used by Schirmer would probably prove the most convenient method for testing sensitiveness for light in the clinic. Merkel[3] compared lights given in succession and obtained a much larger difference as just noticeable,—from one-tenth to one-half of the stimulus. The intensities were adjusted by altering the distance of a lamp from a ground-glass screen.

The paper by König and Brodhun,[4] noticed in the preceding section, was primarily concerned with determining the just noticeable difference. This paper is of special value because colors of the spectrum were used and a large range of intensities was investigated. The research was carried out in v. Helmholtz's laboratory, and full details will be found in the second edition of his "Handbuch." The just noticeable difference for white light was found to be the smallest part of the stimulus (one-sixtieth) when the latter was about ten thousand of the units used (see above), and to remain nearly the same between one thousand and fifty thousand. For greater and less intensities the just noticeable difference was relatively larger, being more than half the stimulus when the intensity was near the threshold. v. Helmholtz[5] accounts for the relative increase of the just noticeable difference with fainter lights by the interference of the idio-retinal light. With strong intensities the just noticeable difference was not affected by

FIG. 6.



[1] Ueber die Gültigkeit des Weber'schen Gesetzes für den Lichtsinn, Arch. f. Ophth., xxxvi. (4) 121–149, 1890.

[2] Loc. cit.

[3] Die Abhängigkeit zwischen Reiz und Empfindung. Erste Abtheilung, Philos. Stud., iv. 541–594, 1888.

[4] Loc. cit.

[5] Loc. cit.

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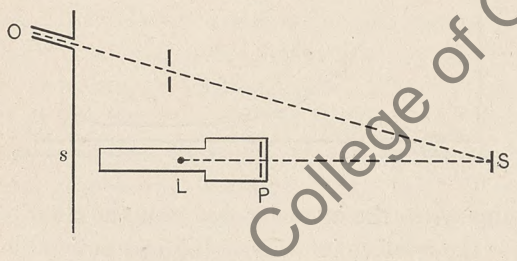
the color of the light; with weak intensities, however, the sensitiveness was greater towards the blue end of the spectrum. The relations are shown in the accompanying curve, in which the abscissæ are proportional to the logarithms of the intensities and the ordinates are proportional to the fraction of the light which was just noticeable. The branch *I* includes all the colors, the branch *II* the red-yellow half of the spectrum, and the branch *III* the blue half.

Results conflicting with these of König and Brodhun and with each other were previously obtained by Lamansky[1] and by Dobrowolsky,[2] who also worked under the direction of v. Helmholtz. According to Lamansky, the sensitiveness is greatest for yellow and green. According to Dobrowolsky, the sensitiveness is greatest for violet, being nearly twenty times as great as for red. v. Helmholtz in the second edition of his "Handbuch" does not mention the experiments by Lamansky and by Dobrowolsky, so he probably considers them superseded by König and Brodhun's research.

Müller-Lyer[3] has published two papers on the just noticeable difference which are of special importance, because they consider the relation of intensity to the area of the field and because they were prepared with a view to practical application in ophthalmology. He used differently illumined disks, and found that as the intensity increases the difference which can be distinguished becomes larger, but more slowly than in direct proportion to the stimulus. The departure was greater for the fovea than for the peripheral parts of the retina.

The most recent experiments concerned with the discrimination of lights were carried out by Fullerton in conjunction with the writer.[4] In these experiments the times of exposure, areas, and other conditions were kept constant. The arrangement of apparatus is shown in the figure.

FIG. 7.



The observer was placed in a separate compartment at *O* and saw the light at *S*. A pendulum at *P* allowed the light to appear at *S* for one second, cut it off for one second, and then allowed it to appear again for one second. While the light was cut off the intensity was altered by shifting the lamp *L*, and the observer was required to decide

[1] Ueber die Grenzen der Empfindlichkeit des Auges für Spectralfarben, Arch. f. Ophth., xvii. (1) 123–134, 1871; also Pogg. Ann. d. Phys. u. Chem., cxliii. 633–643, 1871.

[2] Beiträge zur physiologischen Optik. II. Ueber Empfindlichkeit des Auges gegen verschiedene Spectralfarben, Arch. f. Ophth., xviii. (1) 66–74, 1872.

[3] Ueber die Abhängigkeit der relativen Unterschiedsempfindlichkeit von Intensität und Extension des Reizes, Arch. f. Anat. u. Physiol. (Physiol. Abtheilung), Supplement. Band, 91–140, 1889.

[4] On the Perception of Small Differences, 134–149, Philadelphia, 1892.

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which of the lights was the more intense and assign the confidence felt in his decision. Nine observers were tested, and their accuracy of discrimination was found to vary considerably, the difference which could be correctly distinguished seventy-five per cent. of the time varying between about one-tenth and one-fifth of the light. These results show that tests made in the clinic would indicate individual differences in sensitiveness, and would probably give early indications of certain diseases of the eye and nervous system.

III.—THE COMPARISON OF MAGNITUDES.

The sensitiveness of the visual mechanism and the accuracy of discrimination may be tested not only by measuring the least difference which can be perceived, but also by determining the accuracy with which different intensities can be estimated and compared. In the latter case, however, the judgment of the observer plays a more important part, and the results will be found less accordant and less useful in the clinic. The first attempts to estimate differences in intensity were in the classifications of the magnitudes of the stars. These intensities have since been determined by photometric methods, and it is thus possible to compare the estimated difference with the objective difference. A detailed discussion of the results is given by Müller[1] and by Jastrow.[2] Plateau determined by direct experiment the accuracy with which a shade of gray could be adjusted midway between a lighter and a darker shade, and Delbœuf made similar and more careful determinations with revolving wheels. Revolving wheels, with due allowance for contrast and other disturbing factors, have more recently been used in Wundt's laboratory by Lehmann[3] and by Neiglick.[4] Breton[5] arranged shades of gray so as to make a series of equal differences in intensity. Ebbinghaus[6] carried out similar experiments with greater care and exactness, and Leuba[7] has recently classified artificial stars. Merkel determined the accuracy with which the intensity of lights can be doubled. These experiments on the comparison of magnitudes have been carried out by so many different methods, and the number of observers has been so small, that it is impossible to learn from them how different observers vary, or whether variation would be related to any special condition of the eye or of the nervous system. The experiments have been made with a view to

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[1] Zur Grundlegung der Psychophysik, Berlin, 1878.

[2] The Psycho-physic Law and Star Magnitudes, Am. Journ. of Psych., i. 112–127, 1887.

[3] Ueber die Anwendung der Methode der mittleren Abstufungen auf den Lichtsinn, Philos. Stud., iii. 497–533.

[4] Zur Psychophysik des Lichtsinns, Philos. Stud., iv. 28–111.

[5] Sur la loi de Fechner, Les Mondes (Cosmos), Sér. 2, xxxviii. 63–69.

[6] Die Gesetzmässigkeit der Helligkeit, Sitz.-ber. d. Akad. d. Wissen. zu Berlin, 1887, 995–1009.

[7] A New Instrument for Weber's Law, with Indications of a Law of Sense Memory, Am. Jour. of Psych., v. 370–384, 1893.

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studying the laws of Weber[1] and of Fechner,[2] which we have next to consider.

IV.—WEBER'S LAW.

In describing experiments on the just noticeable difference it has been stated that the addition of a certain part, say $\frac{1}{100}$, of the light, could be distinguished, not that a fixed difference, say $\frac{1}{100}$ of the light of a candle, could be distinguished. Weber's law states as a general proposition that the least difference which can be distinguished is a proportional part of the intensity of the stimulus. Thus, if in a room lit up by a hundred candles the introduction of an additional candle made the illumination just perceptibly greater, when the room was lit up by one thousand candles the introduction of an additional candle would not be perceived, but ten candles would be required to make a difference which could just be distinguished. This relation was first noticed by Bouguer,[3] but its statement is usually called Weber's law, as Weber[4] extended its application to different senses. The experimental study of Weber's law, and the attempt to apply it to the measurement of the intensity of sensation, have received much attention from physiologists, physicists, and psychologists. Indeed, it would be difficult to mention another subject so limited in range which has been so largely contributed to by men eminent in different departments of science. In this place we are concerned with vision only, but it may be worth while to give for comparison results concerning other senses obtained by various observers. The fraction gives approximately the part of the stimulus which could be correctly distinguished seventy-five per cent. of the time. This is the probable error of mathematics. Where writers have determined the difference they think they can just notice we have no definite standard for comparison, but we may assume perhaps that they would distinguish such a difference correctly about nine times out of ten trials, and deduce the probable error from this relation. Extreme values, such as are obtained with very weak stimuli, are omitted.

Simultaneous lights	$\frac{1}{30}-\frac{1}{200}$
Successive lights	$\frac{1}{5}-\frac{1}{10}$
Sounds	$\frac{1}{3}-\frac{1}{4}$
Pressures on skin	$\frac{1}{3}-\frac{1}{30}$
Lifted weights	$\frac{1}{12}-\frac{1}{40}$
Force of movement	$\frac{1}{8}-\frac{1}{40}$
Time of movement	$\frac{1}{6}-\frac{1}{17}$
Extent of movement	$\frac{1}{7}-\frac{1}{120}$
Length of lines (by the eye)	$\frac{1}{30}-\frac{1}{100}$
Temperature	$\frac{1}{5}-\frac{1}{10}$° R.

[1] Annotationes de Pulsu, Resorptione, Auditu et Tactu, Lipsiæ, 1834; Der Tastsinn und das Gemeingefühl, in Wagner's Handwörterbuch der Physiologie, iii. 2, Braunschweig, 1846; Annotationes Anatomicæ et Physiologicæ, Lipsiæ, 1851.

[2] Zend Avesta, Leipzig, 1860; In Sachen der Psychophysik, 1877; Elemente der Psychophysik, Leipzig, 1860; Revision der Hauptpunkte der Psychophysik, Leipzig, 1882.

[3] Loc. cit. [4] Loc. cit.

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It follows from the above that sight is the most delicate of the senses when the lights are given side by side and can be compared, but that when the lights are successive (as must be the case with sounds, movements, etc.) the accuracy of perception seems to be no greater than for other senses.

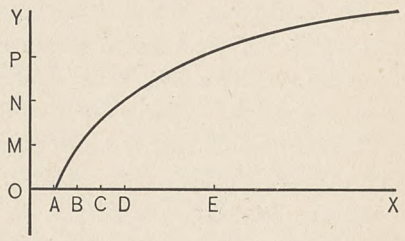
If Weber's law do in fact obtain, we can conveniently compare different senses and different observers. If, however, the just noticeable difference vary with the intensity of the stimulus, it is difficult to decide when stimuli of different sorts are equal in intensity, and consequently different observers must be tested with stimuli of the same intensity. It has always been found that Weber's law fails near the threshold, the just noticeable difference becoming a larger part of the stimulus, but this may be explained by the interference of faint stimuli which continually affect the sense organ, such as the idio-retinal light of the eye, noises in the air, etc. With very strong stimuli Weber's law also fails, but this may be due to injury of the sense organ, which would interfere with its sensitiveness. Whether or not Weber's law holds for intermediate intensities is still an open question, but the weight of testimony seems to incline to the conclusion that its validity is at most only approximate.

The difference in intensity which can just be distinguished is a function not only of the absolute brightness of the lights but also of their area and time-relations. These factors have not been properly distinguished in most researches on the accuracy of perception, and the varying results are thus to a considerable extent explained.

V.—FECHNER'S LAW.

The results of the experiments on the just noticeable difference have been explained by Fechner in such a manner as to make it possible to measure the intensity of sensation and to determine a correlation between mental and physical changes. Fechner assumes that the just noticeable difference is an equal mental magnitude for every intensity of the stimulus, whence it follows that as the intensity of the stimulus is increased it has a relatively decreasing effect in consciousness. This relation is shown in the accompanying curve (Fig. 8). The subdivisions of the horizontal axis represent equal increments in the intensity of the stimulus, and the subdivisions of the vertical axis represent the series of differences which can just be perceived, and these are assumed to be equal increments to the intensity of sensation. When the stimulus is very weak there is, as we have seen, no appreciable sensation, and this is shown in the figure as the curve crosses the horizontal axis at *A*. With this stimulus the sensation crosses the thresh-

FIG. 8.



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old of consciousness. When the stimulus is increased by the amount AB and is equal to OB, there is an increase in intensity of sensation, OM, which can just be noticed. When, however, the stimulus is further increased by BC, which is equal to AB, no distinct change in consciousness occurs, but the stimulus must be increased by an amount greater than AB, say BD, in order that the change in sensation, MN, may be just noticeable. And thus as the intensity of the stimulus is greater the increment which can just be noticed continually increases. Fechner deduces the relation between sensation and stimulus mathematically as follows: If the just noticeable difference be a proportional part of the stimulus, then

$$(1)\quad N = C\frac{s}{S},$$

in which N is the just noticeable difference and is assumed by Fechner to be a constant mental magnitude for every value of the stimulus. S is the intensity of the stimulus, s the increment in the stimulus which can just be noticed, and C a constant which might vary for different senses, individuals, etc. Supposing the above equation to hold for very small changes, it may be written

$$(2)\quad dN = C\frac{ds}{S},$$

and by integration

$$(3)\quad N = C \log s + A.$$

The constant A may be determined at the threshold, where $N = 0$. In this case

$$(4)\quad C \log a + A = 0.$$
$$(5)\quad A = -C \log a.$$

If we take the intensity of the stimulus at the threshold as unity, $a = 1$, we may write (3)

$$(6)\quad N = C \log s;$$

that is, the intensity of sensation is equal to the logarithm of the intensity of the stimulus multiplied by a constant.

Fechner's deduction is open to the criticism (in addition to the question of the validity of Weber's law) that the just noticeable difference is not a unit which may be used to measure sensation. On the supposition that it is correct, we may ask, Why should the sensation increase as the logarithm of the stimulus? Three answers have been given to this question. Fechner himself holds that his law expresses an ultimate relation between mind and matter. Others (*e.g.*, Müller,[1] Bernstein,[2] Ward[3]) maintain that the sensation, indeed, varies directly as the brain-changes correlated with it, but that these increase as the logarithm of the stimulus. Wundt argues that we are concerned with an estimation which is subject to the so-called "law

[1] Loc. cit.

[2] Untersuchungen über den Erregungsvorgang im Nerven- und Muskel-Systeme, Heidelberg, 1871.

[3] An Attempt to interpret Fechner's Law, Mind, i. 452–466, 1876.

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of relativity:" a pound would not be a considerable addition to the weight of a man, but would greatly alter the weight of a pigeon. Bernoulli,[1] as long ago as 1730, pointed out that the value of money is relative (*e.g.*, to a man having an income of $1000, $1 will have as much value as $10 to a man having an income of $10,000), and deduced a formula exactly analogous to Fechner's,—namely, the worth of money to the individual increases as the logarithm of its amount.

VI.—METHODS FOR STUDYING THE ACCURACY OF PERCEPTION.

It is desirable to consider in this place the methods which have been developed in researches on the relation between intensity of stimulus and intensity of sensation. These methods are to a certain extent analogous to those required for the adjustment of observations in the physical sciences. There is, however, this important difference: physical science aims at eliminating errors of observation; psychology aims at studying their nature. In ophthalmology and many other branches of medicine the physician has the task both of the physicist and of the psychologist. On the one hand, he must determine from different and conflicting observations the true state of the case; on the other hand, it is the error or anomaly of the patient which must be studied in order that it may be cured or corrected. It must be admitted that physicians have hitherto depended chiefly on insight and experience rather than on measurement: medicine has been an art, not a science. But considerable changes have recently taken place, and the student with the help of scientific methods can often make a diagnosis as correctly as the older physician with years of experience.

Methods for studying the perception of small differences may be of two sorts: they may seek to determine the accuracy with which an observer can estimate a difference, or they may seek to determine his error of observation. The former method depends on the judgment of the observer, and lacks an objective criterion. Most of the experiments on the intensity of lights considered above were made by this method, and it is the one the physician mostly uses, as when he asks his patient, Do you feel better to-day than yesterday? Does it hurt when I prick you with this pin? But the physician depends as little as possible on the answer of the patient; he seeks to observe for himself whether the patient appears better or worse, whether he shows signs of pain when pricked. The error of observation is now transferred to the physician, and is lessened by his experience, skill, and insight. Still, the physician prefers an objective standard, as the use of a thermometer, or the action of the patient when he is in fact pricked and when there is only a pretence to prick. Great advances have been made in the objective study of the eye with the aid of the ophthalmoscope, the optometer, the skiascope, etc., but in the correction of defects of refraction and in the diagnosis of many diseases the perceptions of the patient and the

[1] Cf. Todhunter's History of the Theory of Probability, Cambridge and London, 1865.

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account he gives of them are important data for the physician. It is desirable, therefore, to know the best methods for obtaining these data, and the reliance which can be placed on them.

Two objective methods for the study of the perception of small differences may be distinguished: (1) the method of average error, and (2) the method of right and wrong cases. In using the method of average error the observer is given a stimulus—say a light of a certain intensity—and is required to adjust a second light until it appears the same. The second light will usually be too great or too small, and the error of the observer is determined. The experiment is repeated a number of times, and the average error measures the accuracy of discrimination. The reliability of the result increases as the square root of the number of trials. In using the method of right and wrong cases two lights nearly alike in intensity are shown to the observer, and he is required to say which appears the brighter. He will be sometimes right and sometimes wrong in his judgment, and from the ratio of right to wrong cases the accuracy of discrimination may be determined.

The method of right and wrong cases is extensively used in ophthalmology, but not with as great exactness as is usual in psychological research. The methods of the laboratory must of necessity be simplified in the clinic, but the careful scientific study of conditions in a medical course would make clinical examination quicker as well as more exact. Thus, when it is found that a patient can just read the test letters under the conditions employed, it may be asked what is meant by "just read." Probably not that the patient will never make a mistake, for if the trial be continued mistakes will occur even with letters which can be distinctly seen. The physician doubtless fixes some standard in his mind, say that the answer of the patient shall be correct nine times out of ten, but he rarely records the results of the separate trials, and supposing two mistakes to be made in ten trials he would scarcely know how to prescribe glasses which would enable the observer to make one mistake only in ten trials. Yet the theory of probability makes this possible. When the method of right and wrong cases is used scientifically the theory of probability also enables the physician to know how nearly his correction is exact; he can assign its probable error,—that is, the limits within which it is likely that the prescription is exactly correct.

In conclusion, two precautions in method may be mentioned which psychological research has emphasized. In the first place, we can perceive a thing better when we know what it is. The memory image is added to the immediate perception, and in our daily life we can scarcely distinguish the part played by each. In the second place, it is necessary to recognize unconscious memory. A series of letters can be learned more quickly or seen more readily when it has once been used. The patient should, therefore, always be ignorant of the test used, and the same series of impressions should not be repeated.

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Psychological methods are discussed by Fechner,[1] Müller,[2] Wundt,[3] Fullerton and Cattell,[4] and others. The psychological aspects of perception and memory are treated in a full and interesting manner by James.[5]

VII.—INTENSITY AND COLOR.

The different colors of the sun's spectrum do not appear of the same intensity. As Newton remarked, "The most luminous of the prismatic colors are the yellow and orange, . . . and next to these in strength are the red and green." The varying intensity of the several colors was first investigated by Fraunhofer,[6] and later by Vierordt.[7] Fraunhofer compared the colors of the sun's spectrum directly with colorless light. According to his results, if the intensity of yellow be placed at 1000, the intensity of the other colors will be red (B) 32, orange (C) 94, green (E) 480, blue (G) 31, and violet (H) 5.6. Vierordt determined the amount of white light which could be mixed with the several colors without producing a noticeable decrease in saturation. By this method he obtained as coefficients of intensity, red 22, orange 128, yellow 1000, green 370, blue 8, violet 0.7. For the spectrum of a gas flame the intensities of the orange and red were greater and of the green and blue less. Rood has recently made an important advance in chromophotometry by comparing the intensities of colors by means of the flickering of revolving wheels. This method obviates the difficulties in the way of the comparison of disparate sensations.

The direct comparison of the intensity of different colors is difficult, and observers differ greatly in the confidence with which they make such comparisons. Careful and important experiments on the subject have been made during the past few years in v. Helmholtz's laboratory by König, Brodhun, and Dieterici. These are, however, largely concerned with working out three possible fundamental colors, and only partly fall within the limits of this article. Brodhun,[8] who is color-blind for red, seems able to compare the brightness of different colors with less variation than observers with normal color-vision.

When the objective intensity is altered, different colors do not maintain the same relations of brightness. It was noticed by Purkinje that if red and blue be taken, which seem to be of about the same intensity, and the illumination of each be reduced equally, the blue can be seen the longer. In general the less refrangible colors appear relatively brighter in a strong light and the more refrangible colors brighter in a faint light.

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[1] Loc. cit. [2] Loc. cit. [3] Loc. cit. [4] Loc. cit.

[5] The Principles of Psychology, 2 vols., New York, 1890.

[6] Bestimmung des Brechungs- und Farbenzerstreuungs-Vermögens verschiedener Glasarten in Bezug auf die Vervollkommnung achromatischer Fernröhre (Denkschriften der Bayrischen Akademie, München, 193, 1815.)

[7] Anwendung des Spectralapparates zur Messung und Vergleichung der Stärke des farbigen Lichtes, Tübingen, 1871.

[8] Beiträge zur Farbenlehre, Inaug. Diss., Berlin, 1887.

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König[1] has recently investigated Purkinje's phenomenon and the brightness of colors of the spectrum with different absolute intensities. He used eight different intensities, the strongest of which was 262144 times as great as the weakest. He found Purkinje's phenomenon to be much more pronounced for weak than for strong intensities. A further complication follows from the fact (demonstrated by Van der Weyde and by Brodhun) that if a spectrum color be matched by a mixture of two colors and the intensity altered, the colors will be no longer alike. It had previously been discovered by Preyer and König that the position of the neutral point of color-blind observers alters with the intensity. Ebbinghaus[2] has further found that grays of the same intensity, made by combining different pairs of complementary colors, do not remain of the same intensity when the illumination of both grays is altered equally.

The alterations in color due to changing intensity greatly affect the appearance of natural objects. In a general way increasing the intensity makes colors more yellowish, decreasing the intensity makes colors more bluish. Thus, grass in the sunlight looks yellowish-green, while the part of the same plot of grass on which the shadow falls looks bluish-green. The general effect of a sunny day is yellowish, and that of a clouded day, or of twilight, bluish. A moonlight scene is still more distinctly bluish, and painters use blue tones to represent such a scene. We can obtain the effects of a cloudy day by looking through a bluish glass on a sunny day, and the converse effects by using a yellowish glass. A pure gray looks bluish when compared with white. Rood[3] found it necessary to add seventeen per cent. of indigo to white in order to obtain the color-tone of gray made by adding fifty per cent. of black.

When the illumination is very intense or very faint, colors disappear altogether, or perhaps it should be said that when intensely illumined they become a yellowish-white, and when faintly illumined a bluish-gray. We have already considered the threshold for color. Before colors disappear their tone is altered. Thus, if the light of the sun's spectrum be gradually diminished, the colors will disappear, except red, green, and violet-blue. These colors then become red-brown, olive-brown, and blue-gray, and finally disappear, the entire spectrum becoming gray. When the intensity is very great, violet is the first of the colors to become white, blue becomes violet, and green yellowish, before the colors disappear. Red is said to remain yellowish with the greatest intensity. In this gray spectrum the maximum of intensity is at a wave-length of 535 $\mu\mu$.

According to v. Helmholtz, these relations of color and intensity are brought into harmony with the theory of three fundamental colors and

[1] Ueber den Helligkeitswert der Spektralfarben, Beiträge zur Psychologie und Physiologie der Sinnesorgane, H. v. Helmholtz als Festgruss, etc., Hamburg and Leipzig, 1891, 311–388.

[2] Theorie des Farbensinnes, Zeitsch. für Psychol., v. 145–238, May, 1893.

[3] Loc. cit.

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nerve-fibres by assuming that the relative effects of the components of the colors on the three sets of fibres vary with the intensity. It seems, however, to the writer that the facts are not explained by the theory, but rather that unlikely hypotheses are made in order that the facts may not be subversive of the theory. Hering's theory, which in general is more satisfactory from the point of view of psychology, fails to account for the intricate relations of intensity and color.

VIII.—INTENSITY AND SHARPNESS OF SIGHT.

If Weber's law were exactly correct, differences would be equally apparent whatever the intensity of the light, and a printed page could be read equally well in any illumination. Weber's law does not hold for very faint nor for very strong intensities, and a printed page cannot be read as well in twilight or in direct sunlight as in ordinary daylight. The relation of intensity of illumination to sharpness of sight is important in practical ophthalmology, as it is necessary to know what illumination is the most favorable for reading test-types, etc., and what corrections must be made for other illuminations. It would also be of great importance to determine what intensity of light is most suitable and advantageous to the eyes in reading and in other tasks requiring near fixation. The writer believes that polarized light may be irritating and destructive to the skin and the eyes, but this has not been investigated. The relation between intensity and sharpness of sight has been studied by several observers, of whom it is necessary to mention here only Macé de Lépinay and W. Nicati[1] and Uhthoff.[2] The research by the latter was carried out with great care in v. Helmholtz's laboratory. He used the symbols proposed by Snellen for testing sharpness of sight, and also a wire grating. The sharpness of sight increased from 0.13 to 2.37 as the illumination increased, at first rapidly and then more slowly, but the maximum sharpness could not be obtained with the light used. The sharpness of sight differs for the different colors, but this is due chiefly to the inherent difference in brightness of the colors. When a light is used sufficient to give the maximum sharpness of sight, this seems to be the same for the several colors.

IX.—INTENSITY AND THE FIELD OF VISION.

The apparent intensity of light and color varies with the size of the object, the part of the retina affected, and the surrounding field. Lights

[1] Recherches sur la comparaison photométrique des diverses parties d'un même spectre, Ann. de Chem. et de Phys., Sér. 5, xxiv. 289–337, 1881; deuxième Mémoire, Sér. 5, xxx. 145–214, 1883.

[2] Ueber das Abhängigkeitsverhältniss der Sehschärfe von der Beleuchtungsintensität, Arch. f. Ophth., xxxii. (1) 171–204, 1886; Ueber das Abhängigkeitsverhältniss der Sehschärfe von der Intensität so wie von der Wellenlänge im Spektrum, xxxvi. (1) 33–61, 1890; Ueber die kleinsten wahrnehmbaren Gesichtswinkel in den verschiedenen Teilen des Spektrums, Zeitsch. f. Psych., i. 155–160, 1890.

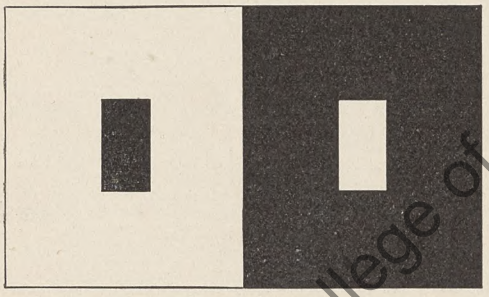
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and colors when very intense can be seen even though they have no appreciable area, as in the case of the stars, whose colors we can distinguish. With moderate intensities, however, colors must have a certain area in order to be seen as light, and a certain greater area in order that the color may be recognized. The fact that colors must have a certain area in order that they may be seen was noticed by Plateau,[1] and the relations have been investigated by Aubert and v. Wittich.[2] In bright but diffused daylight the angle the surface subtends is from 39″ to 11′ 46″. On a black ground the bright colors, yellow and orange, are seen first as "clouds of light." On a white ground the different colors are seen at nearly the same angle as dark spots. When a color is very small in area its tone varies, as is the case when the intensity is faint.

The difference in intensity which can just be distinguished depends on the area of the surfaces. Aubert[3] studied the relation with revolving wheels, the area of stimulation being altered by increasing the distance from which the wheels were viewed. Increasing the distance does not alter the brightness of the lights, excepting so far as the rays may be absorbed by the air. With a moderate intensity Aubert found the just noticeable difference increased from one seventy-second to one-eleventh as the angle decreased from 7° to 6° 22′, and with a faint light and a small angle the one ring had to be nine times as bright as the other in order that a difference might be perceived.

Not only is the apparent intensity of lights altered by the area, but the apparent area is altered by the intensity. A brightly illumined object appears larger than an object of the same size less brightly illumined, a phenomenon to which the name irradiation has been given. Thus, in the figure the white square on a black ground appears larger than the black square on the white ground. In the same manner a bright light partly covered by a black screen seems to dip into the screen, as shown in the figure.

FIG. 9.



Irradiation seems to be chiefly due to imperfect accommodation, and is much more marked when the object is not exactly fixed. The diffusion circles of the white cover part of the black field, and the white is thus

[1] Ueber einige Eigenschaften der vom Lichte auf das Gesichtsorgan hervorgebrachten Eindrücke, Pogg. Ann. d. Phys. u. Chem., xx. 304–332, 1830.

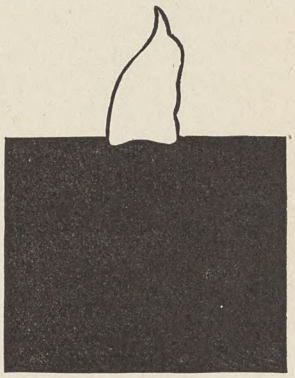
[2] Ueber die geringsten Ausdehnungen welche man farbigen Objecten geben kann, sie noch in ihrer specifischen Farbe wahrzunehmen, Königsberger medicinische Jahrbücher, iv. 23, 1864.

[3] Op. cit.

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enlarged. It is true the white near the edge is darkened by the diffusion circles from the black, but the gray zone is attributed to the white, in accordance with Weber's law. Plateau and others have explained irradiation by assuming that the neighboring elements of the retina are sympathetically affected by the light which does not directly fall upon them; but this supposition does not seem required for the explanation of the phenomenon.

FIG. 10.



The astronomers have noticed that a faint star can be seen best in indirect vision, but this may be because the fovea centralis is fatigued by light reflected from the sides of the telescope. Aubert could not notice any appreciable difference in the intensity of light seen in direct and in indirect vision. Schadow,[1] Kirschmann,[2] and others have published investigations on the relative intensity of lights in direct and in indirect vision, with conflicting results. It seems probable, however, that the peripheral portions of the retina are the more sensitive. The appearance of a color differs greatly according to the part of the retina stimulated, the outer zones being altogether color-blind. The perimeter is now universally used in the clinic, and is the subject of special articles in this work.

The apparent intensity of light and color is greatly influenced by the surroundings. Thus, a gray surface on white appears much darker than on black. These effects of contrast are partly due to movements of the eyes and fatigue, and will be noticed below. The intensity of light is somewhat greater when it affects both eyes than when it affects one only. Jurin's result that the difference in intensity is about one-thirteenth has been confirmed by later observers. An apparently conflicting result is obtained in a curious experiment suggested by Fechner. If we look at a white surface with one eye and then open the other with a smoked glass before it, the field becomes darkened, although the total amount of light has been increased. This experiment is related to the conflict of the fields of vision, which subject is treated elsewhere in this work.

PART II.—TIME.

X.—THE THRESHOLD AND THE MAXIMUM SENSATION.

When the area of a light is very small, or when the intensity is very faint, it cannot be seen. It also holds that a light cannot be seen when its duration is very short. We find, therefore, a threshold of size, a threshold

[1] Die Lichtempfindlichkeit der peripheren Netzhauttheile im Verhältniss zu deren Raum- und Farbensinn, Arch. f. d. ges. Physiol., xix. 439–461, 1879.

[2] Die Farbenempfindung im indirecten Sehen, Philos. Studien, viii. 592–614, 1893.

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of intensity, and a threshold of time. It is of especial interest to physiological and psychological science that these qualities are correlated at the threshold. Thus, the threshold of intensity depends on the area and time of stimulation, and a measurable decrease in intensity is compensated by a measurable increase in area or time. We are, consequently, developing a mechanics of the nervous system and of sensation.

The fact of the threshold of time was first indicated by Plateau and by Fick.[1] If the time of exposure of a white light be gradually shortened, the white will appear gray and will finally disappear. The threshold for white light has not been exactly measured, but investigations with colors have been carried out by several observers,—in the first instance by v. Vierordt[2] and his pupils. They used a pendulum myograph which carries a screen with a vertical opening, the time of exposure being known from the rate at which the pendulum swings and the width of the opening. In order that the light reflected from pigments when the time of exposure was 2.90 σ ($\sigma = .001$ second), it was necessary that the illumination should be from one hundred and seventy-three to five hundred and thirteen times as great as when the time was not limited. As the time was lengthened the intensity decreased, but no definite relation is deduced by the writers. Kunkel[3] in Fick's laboratory made similar experiments with colors of the spectrum. He found the threshold to be different with different colors, and the appearance of the colors to vary with the intensity and time of exposure. Thus, green and even yellow may appear blue. Such changes in color should be compared with those occurring when the intensity is faint and when the area is small. Baxt[4] in v. Helmholtz's laboratory determined the interval which must elapse after an impression has been in view a short time (4.8 σ) in order that it may be obliterated by a following bright light. This time varies with the impression, being 50 σ for a group of letters. The process in this case is complex, but the time may, perhaps, give the difference in the time of perception of the impression used and of a bright light. The writer[5] has published experiments measuring the time threshold for colors, letters, and words. For colors (pigments compared with Chevreul's tables and reflecting daylight from the clear sky) the average times for seven observers were red 1.28, orange 0.82, yellow 0.96, green 1.42, blue 1.21, and

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[1] Ueber den zeitlichen Verlauf der Erregung in der Netzhaut, Arch. f. Anat. u. Physiol., 1863, 739–764.

[2] Das Pendel als Messapparat der Dauer der Gesichtseindrücke, Arch. f. d. ges. Phys., ii. 121–127, 1869. Bruckhardt and C. Faber, Versuche über die zu einer Farbenempfindung erforderliche kleinste Zeit, Arch. f. d. ges. Physiol., ii. 127–142, 1869.

[3] Ueber die Abhängigkeit der Farbenempfindung von der Zeit, Arch. f. d. ges. Physiol., ix. 197–220, 1874.

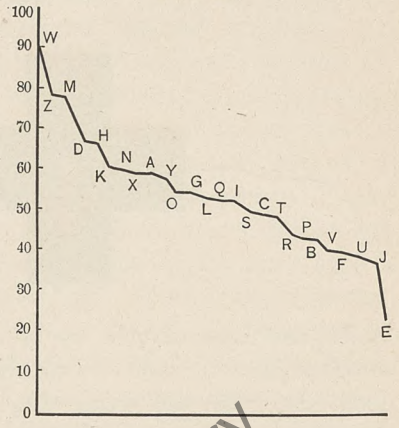
[4] Ueber die Zeit, welche nötig ist, damit ein Gesichtseindruck zum Bewusstsein kommt und über die Grösse (Extension) der bewussten Wahrnehmung bei einem Gesichtseindrucke von gegebener Dauer, Arch. f. d. ges. Physiol., iv. 325–336, 1871.

[5] Ueber die Trägheit der Netzhaut und der Sehcentrums, Philos. Stud., iii. 94–127, 1885; Abridged, Brain, viii. 295–312, 1885–86.

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violet 2.23 σ, the difference being probably influenced by the intensities of the colors. The times tended to increase in arithmetical progression as the intensity of the light decreased in geometrical progression. The times for single letters and for words were about the same, but the times for different types and for the different letters of the same type were not the same. The relative legibility of the several letters was thus determined, and is shown for capital small pica letters in the accompanying curve. The ordinates represent the percentage of times each letter was correctly read in two hundred and seventy trials. E, the letter most frequently used, is thus the most illegible. The relative legibility of the letters is of practical importance, as the more illegible letters could be modified so as to make them more easily read. It is also of interest in this place, owing to the use made of letters in determining defects of accommodation. The letters selected for this purpose should be as nearly as possible equally legible, and it is probable that it would be an advantage to use geometrical forms such as those proposed by Snellen or the series planned by Jastrow and Oliver for the Columbian Exposition. With Snellen's test-types the time of exposure required in order that they should be correctly seen was D = 4, 0.65; D = 1.75, 0.82; D = 1.25, 1.23; D = 0.8, 1.57; D = 0.5, 3.50 σ. It is not unlikely that more accurate results could be obtained in clinical work if the time of exposure were measured.

FIG. 11.



When the time of exposure is made greater than the threshold, the intensity of the sensation increases, and when the time is in the neighborhood of one-fifth second the sensation reaches a maximum. This can be seen by cutting a narrow opening (five millimetres by five centimetres) in a black screen and jerking the screen over small pieces of colored paper. When the movement is quick and the time of exposure very short (the threshold), no color can be seen; as the time is increased the color becomes brighter and brighter, and when the time is one-tenth to one-half second the color seems brighter than the same color does in ordinary vision. A landscape looked at in this way appears unusually brilliant. Brücke,[1] with revolving wheels, found the maximum sensation to occur when the time of stimulation was 189 σ for intermittent lights. More extended measurements with white lights have been made by Exner,[2] and with colored light by

[1] Ueber den Nutzeffect intermittierender Netzhautreizungen, Sitzungsber. d. Wiener Akad., Math.-Natur., lxix. (2) 128–153, 1864.

[2] Ueber die zu einer Gesichtswahrnehmung nöthige Zeit, Sitzungsber. d. Wiener Akad., Math.-Natur., lviii. (2) 601–632, 1868.

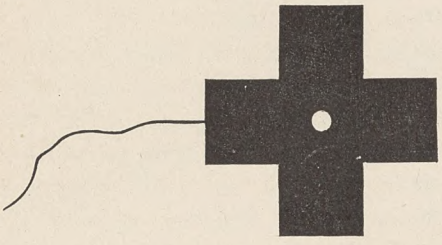
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Kunkel.[1] The former found the times to decrease in arithmetical progression as the intensity of the light is increased in geometrical progression. The latter found the times for colors reduced to about the same intensity to be red 57, green 133, and blue 92 σ.

XI.—FATIGUE.

When the time of exposure is still further increased, the sensation begins to fade, and finally loses its quality and may disappear altogether. The effects of fatigue may be seen by placing a small black cross, as shown in Fig. 12, on a sheet of white paper. If after looking at the cross for ten seconds it be jerked away by the thread, a very white cross will be seen on the sheet of paper. The eye has become fatigued for the white excepting the part covered by the cross, which consequently appears the brighter. The same experiment may be made for colors by placing the black cross on a sheet of colored paper. The part which had been covered by the cross will look much more intense and saturated than the rest. In making such experiments a halo is usually seen about the cross, this being due to involuntary movements of the eyes. According to Fechner,[2] a bright white light (as white paper in the sunlight) does not simply become less bright, but passes through a series of colors. The white at first looks yellow, then blue-green or blue, and finally red-violet or red. These changes in color are thought by Fechner to be due to some of the components of white light producing fatigue sooner than the others.

FIG. 12.



Hess[3] has recently made a complete study of the appearance of spectrum colors after the eye had previously been fatigued for certain colors. He used nine points in the spectrum and two combinations of red and violet, and was able to obtain quantitative results. He thinks the alterations do not accord with the requirements of v. Helmholtz's color triangle.

If a small colored bit be placed on a sheet of gray paper it can be looked at until the color disappears altogether. As first shown by Maria Bokowa,[4] fatigue amounting to color-blindness may be brought about by

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[1] Ueber die Abhängigkeit der Farbenempfindung von der Zeit, Archiv. f. d. ges. Physiol., ix. 197, 1874.

[2] Ueber die subjectiven Nachbilder und Nebenbilder, Pogg. Ann. d. Phys. u. Chem., l. 193–221, 427–470, 1840.

[3] Ueber die Tonänderungen der Spectralfarben durch Ermüdung der Netzhaut mit homogenem Lichte, Arch. f. Ophth., xxxvi. (1) 1–32, 1890.

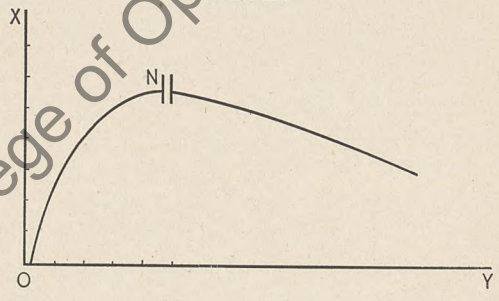
[4] Ein Verfahren künstliche Farbenblindheit hervorzubringen, Zeitsch. f. ration. Med. 3. Reihe, xvii. 161–165, 1863.

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wearing spectacles with colored glasses, all side-light being cut off. Indeed, the same fact is illustrated by comparing our sensation on going from the daylight into a room lit up by gas or lamps with that which we have in the same room in the evening. In the former case the light seems reddish, in the latter we notice no color. Quantitative determinations of fatigue have been obtained by C. F. Müller[1] in Fick's laboratory, by Exner, and by Schön.[2] According to Müller, if the intensity of the original sensation be 1, the intensity after three seconds will be 0.72, after five seconds 0.66, after ten seconds 0.49, after fifteen seconds 0.46, after twenty seconds 0.43, after twenty-five seconds 0.37, and after thirty seconds 0.35. Fatigue consequently follows most rapidly at first, and more slowly afterwards, the apparent intensity waning to half in about ten seconds. Fullerton and the writer have found that when two lights are viewed in succession the second is apt to appear the fainter, the constant error being on the average one-twelfth of the light. Schön used colors of the spectrum and obtained results corresponding to Müller's. After three seconds red decreased to 0.59, green to 0.52, and blue to 0.37. The visual mechanism is most sensitive when we first awake in the morning. According to Müller, the sensitiveness decreases during the day, and objects appear only half as bright in the evening as in the early morning. If this were the case, the time of day should be considered in making tests for the sharpness of vision. Recent experiments by Fick and Grüber, however, show that fatigue reaches its maximum in three-quarters of an hour or less after awakening, and that so long as the light is kept constant no further decrease in sensitiveness occurs in the course of the day. These writers hold that the sensitiveness of the retina is restored by movements of the eyelids and of accommodation; but this view seems to be refuted by Hering.

The relation of the sensation to the time of stimulation is shown in the accompanying curve. The abscissæ represent the time of stimulation, and the ordinates the intensity of the corresponding sensation. The curve is divided in two, the right-hand half being drawn in a different scale as regards time. The curve shows that a short time elapses before there is any sensation, the sensation then increases with the time, at first rapidly and then more slowly, to a maximum, and afterwards begins to wane, and more slowly as the time becomes longer.

FIG. 13.



[1] Versuche über den Verlauf der Netzhautermüdung, Inaug. Diss., Zürich, 1866.

[2] Einfluss der Ermüdung auf die Farbenempfindung, Arch. f. Ophth., xx. (2) 273–286, 1874.

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The threshold and the maximum sensation are accounted for by the principles of inertia. It requires a certain amount of energy to set the visual mechanism in motion, and a certain further amount of energy to excite it fully. The correlation between intensity, extensity, and time may thus be understood, for we are concerned with the total amount of energy which may be contributed chiefly by greater force, increased size, or longer time. Thus, with the intense light of the electric spark objects may be seen, although the time of exposure be very short, whereas a faint star can be seen only after looking for some time at the point in the heavens at which it will appear. The waning of the sensation as the stimulation is continued is accounted for in a satisfactory manner by fatigue and exhaustion. We can understand that the substance in the retina (supposing light to start a nervous impulse by chemical action) may become decomposed during stimulation faster than it can be built up by the cells, as a photographic film becomes less sensitive as it is exposed to the light. The exhaustion may be also of brain-centres. The waning of the sensation as the time of stimulation continues is somewhat analogous to the relations of intensity reviewed in the first part of this article. We saw that the sensation seemed to increase more slowly than the energy of the stimulus.

The times which we have been considering would undoubtedly vary with the condition of the eye and of the nervous system, but, unfortunately, we do not know anything at present about the relations. The time of exposure required in order that a color may be recognized would be an accurate test and measure of color-blindness. The rate of fatigue and restoration would probably be affected by disease of the eye and of the nervous system, and might prove surprisingly useful in diagnosis.

XII.—POSITIVE AFTER-IMAGES.

The same principles of inertia which demand a certain time to set the nervous mechanism in motion would lead us to expect that this motion will continue after the stimulation ceases. We in fact find that a rocket or a meteor is seen as a line of light, due to the impression persisting after the stimulation is no longer present. Aristotle, who has in so many cases anticipated the results of modern science, seems to have first described after-images, and with great exactness. The next reference to the subject seems to be by Augustine; then, after a long interval, Pieresc (1634) described the positive and negative after-image of the window cross-bar, and the subject attracted the attention of Mariotte, Newton, Buffon, Darwin, Goethe, and others. Our present knowledge of the subject we owe largely to Plateau,[1] Fechner,[2] Seguin,[3] Aubert,[4] and v. Helmholtz.[5] In spite of the

[1] Loc. cit.

[2] Loc. cit.

[3] Recherches sur les couleurs accidentelles, Ann. de Chem. et de Phys., Sér. 3, xli. 413–431, 1854; Mémoires sur les couleurs accidentelles, Compt. rend. de l'Acad. des Sciences, xxxiii. 642–644, 1851; xxxiv. 767, 768, 1852; xxxv. 476, 1852.

[4] Loc. cit.

[5] Loc. cit.

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large amount of work which has been devoted to the investigation of after-images—v. Helmholtz gives twenty-four references, which number might readily be doubled—the results are far from being accordant or complete. After-images are, indeed, peculiarly difficult to investigate, because a great deal of practice is required before they can be properly observed, whereas the eyes are apt to be injured by such observations. Fechner's experiments entailed the loss of his eyesight, and several other observers have injured their eyes in studying after-images and entoptic phenomena. Those undertaking the investigation of these subjects should continue their work for a series of years and make only a few observations at one time.

In order to observe a positive after-image, a bright object, as the sun or the globe of a lamp, should be looked at for a short time, say one-half second. This can be done conveniently by holding a black screen (pierced in order to secure a point of fixation) before the eyes and uncovering the object for a moment. The eyes should be rested (closed and covered) for from one to five minutes previously, so that traces of previous after-images may disappear and nothing be left in the field of vision excepting the light chaos or "own light" of the eye. Care should be taken to avoid movements of the eye or body. Observers often find it difficult to notice after-images at first, but my students have always been able to see them after a little practice.

The positive after-image maintains the same relations of light and shade as the original objects, and the colors may be the same at first, but these quickly change. When the eyes are covered after exposure to a bright object, nothing is seen at first by most observers, but after a couple of seconds the after-image appears in the light chaos of the field of vision. v. Helmholtz holds that the delay in the appearance of the after-image is due to movements of the eyes and body; but this can scarcely be the case, as the after-image does not appear at once, even when no appreciable movements are made, and does appear in due time, although movements be purposely made. Indeed, according to recent observations by Hess, the effects of the stimulus disappear almost immediately and give place to a negative after-image (difficult to notice), and this is followed by the positive after-image, which we are here considering. v. Vintschgau and Lustig have also measured the latent period of an after-image.[1]

In the after-image details can often be noticed which, owing to lack of time or to intense brightness, were not seen in the original object. Thus, the twigs of a tree may be imperceptible when they are between the eyes and the sun, but may become apparent in the after-image. As the image fades, the relations of light and shade change, the brighter parts lasting the longer. The further course of the positive after-image becomes complicated with the results of fatigue or exhaustion, and its consideration must be postponed until negative after-images have been noticed.

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[1] Zeitmessende Beobachtungen über die Wahrnehmung des sich entwickelnden positiven Nachbildes eines electrischen Funkens, Arch. f. d. ges. Phys., xxxiii. 494–512, 1884.

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XIII.—NEGATIVE AND COMPLEMENTARY AFTER-IMAGES.

When an object is not very bright and is looked at for several seconds or longer, the positive after-image can be perceived with difficulty or not at all, but the stimulation leaves effects which are called negative after-images. In these, as in the negative plate of a photograph, the relations of light and shade are reversed, so that a bright object on a dark background becomes a dark object on a bright background. Such negative after-images we have already met in the section on fatigue. They can also be seen in the field of vision when the eyes are closed, or can be projected on any surface.

The color of the negative after-image is in normal cases complementary to the color of the original object. It is a curious and important fact that in the case of red the after-image may be positive and complementary. Fechner[1] has made the most careful study of the color of negative after-images, considering the background on which the object is exhibited and the color of the field on which it is projected.

While the color of the negative after-image may be said to be complementary to the color of the original light, it is not established that the relation is exact, and cases have been recorded[2] in which it does not hold at all. Hilbert[3] has recently described his own case, in which the color of the after-image is entirely altered when he is fatigued. It is possible that the nature and course of after-images may prove unexpectedly useful in the diagnosis of certain diseases of the eye and of the nervous system.

The complementary color of negative after-images is accounted for in a general way by fatigue: the eye has become exhausted for the color at which it has been looking, and the complementary components of white light produce relatively greater effects. When the after-image is projected on a colored field complementary to the original light, the color (even of the sun's spectrum) appears brighter and more saturated than otherwise. Colors more intense and beautiful than can be imagined may be seen by looking for one-fourth second at a part of the spectrum early in the morning after the night's rest, the eyes having previously been exposed for one minute to the complementary color.

The longer the time of fixation the longer does the negative after-image last; indeed, Purkinje goes so far as to state that there is an exact proportion, each additional second of fixation (of a candle) increasing the duration of the after-image twenty seconds. Aubert found that when the sun was regarded for three seconds the after-image lasted two-thirds of a minute; when the time of regard was five seconds the image lasted about five minutes; when eight seconds, it was about ten minutes. The after-image also lasts the longer the brighter the light of the original object. In the writer's laboratory exact measurements are being made of the

[1] Loc. cit.

[2] Cf. Aubert, Physiol. Optik, p. 562.

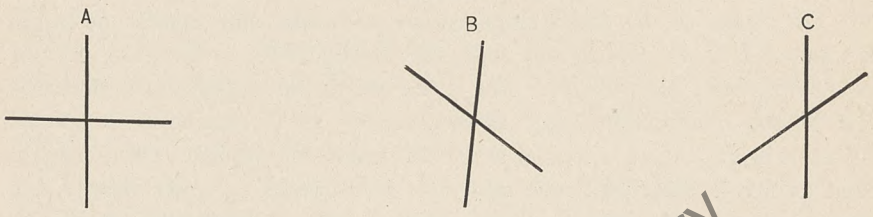
[3] Zur Kenntniss des successiven Kontrastes, Zeitsch. f. Psychol., iv. 74–77, 1892.

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duration of after-images regarded as a function of the time, intensity, and area of stimulation. The average duration of the after-image increased from eight to fourteen seconds as the time of exposure was increased from three to twenty seconds, and from eight to sixty seconds as the intensity of the light was increased three-hundred-and-twenty-fold.

The apparent size of the after-image depends on the distance of the field on which it is projected: thus, the after-image of a surface one centimetre square, regarded at a distance of thirty centimetres, when projected on a wall appears enlarged in proportion to the distance of the wall. This is, of course, explained by the fact that a small object near by stimulates the same area on the retina as a larger object farther away. If the after-image from a surface one centimetre square cover as much space on a distant wall as a picture, we judge it to be as large as the picture. The shape of an after-image, as of a cross or a circle, is distorted when it is projected on an oblique surface. Thus, the after-image of a cross *A* (Fig. 14) will appear

FIG. 14.



as *B* when projected on the wall above and to the left of the observer; to the right it will appear as *C*. This is the converse of the fact that in our daily life a distorted image in this position would be the result of a true cross, and would be interpreted as a true cross.

After-images are not usually observed, it being a psychological law that we attend only to those things which interest us. Sometimes people notice after-images or entoptic phenomena late in life for the first time, and fancy that something is wrong with their eyesight, and may even consult a physician. The physician should, consequently, be prepared to explain how far these phenomena are normal. While after-images are not distinctly distinguished, yet they must greatly alter the appearance of the external world. Thus, moving objects are fused, and produce a total result which consciousness is unable to analyze. Not only so, but, our eyes being constantly in motion, the appearance of objects is greatly altered by what we have previously looked at. We, to a large degree, correct for these alterations; we need to perceive the same objective things as the same, and do so to a considerable extent in spite of subjective differences. But to all of us a piece of gray paper on a white surface looks darker than the same gray on black paper. This is partly due to movements of the eyes; the parts of the retina which had been exhausted by white are not so effectively stimulated by the gray as those parts which had been rested by looking at

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black. In the same manner red looks much brighter on a green surface than on an orange surface. These results persist even when care is taken not to move the eyes, and are termed "contrast." But the phenomena are evidently not explained by naming them. Hering maintains that the excitation spreads in the retina, so that not only the parts stimulated by white but also the neighboring parts are exhausted. v. Helmholtz, on the other hand, maintains that the alterations are due to mistaken judgment, our perceptions being relative. Thus, a medium-sized man may seem tall in the company of a short man and short in the company of a tall man. The effects of contrast are probably determined by various causes, some of which we do not understand. The subject is very important for the artist, especially for the painter, who must depend on contrast to secure light and color. Thus, a painted scene by sunlight is far less bright and a scene by moonlight far brighter than nature, the effects being secured by proper attention to contrast. The subject of contrast is treated elsewhere in this work.

XIV.—THE COMPLICATION OF POSITIVE AND NEGATIVE AFTER-IMAGES.

The course of the after-image is not so simple and regular as might be supposed from reading the accounts usually given in the text-books of psychology and physiology. Nor is the theoretical explanation offered by the Young-Helmholtz theory as satisfactory as is commonly supposed. When a bright object is looked at for an instant the positive after-image is seen as above described, and may not be followed by other images, and when a rather faint color (as a pigment in diffused daylight) is looked at for some time the negative and complementary after-image is seen without further complications. But very striking results may follow the fixation of a white light. These have been described by Plateau, Fechner, Seguin, v. Helmholtz, and Aubert. If bright white light be looked at for a moment, according to v. Helmholtz, there will be a white after-image which passes quickly through a green-blue to a brilliant indigo-blue and then into violet or rose. Then follows a gray-orange, the after-image usually disappearing or becoming negative. In the latter case the orange may be followed by a dim yellow-green. The order and nature of the colors vary according to the time of exposure and the intensity of the light. Admitting light or projecting the image on a brighter field advances the course of the image, and, conversely, decreasing the light brings it back to an earlier stage. If the sun be viewed for an instant, similar results follow, but there are concentric rings of color which proceed from the outside towards the centre. Owing to imperfect fixation and accommodation (and, it may be, to the spreading of stimulation on the retina), the image extends beyond the true disk of the sun, and, the outer circles being less intense, the after-image proceeds more rapidly through its phases.

The descriptions of Fechner and v. Helmholtz seem largely to ignore oscillations of the after-image, ascribing such as occur to accidental movements, pressures, and changes of illumination. The oscillations have, how-

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ever, been properly described by Purkinje, Plateau, and Aubert, and are to the writer the most striking of all the phenomena. These authors have noted four or five oscillations from positive to negative, the after-image lasting in all about five minutes. The writer has made the unexpected observation that an after-image may last indefinitely, the oscillations from positive to negative being innumerable. The writer obtained (after resting the eyes five minutes and exposing them for one minute) an after-image of the clear sky and the bars of a window, which can be seen at the present writing, after an interval of eight months. During the first hour the oscillations occurred continually, at first at intervals of about ten seconds, the panes and bars displaying brilliant and beautiful colors, mostly greens and purples. In the course of the first month the after-image became gradually less distinct. On closing the eyes it always appeared positive, becoming negative after a few seconds, and passing through a series of oscillations which could be continued indefinitely by altering the illumination. Since that time the after-image has become continually less distinct. On closing the eyes it always appears positive, becoming negative only so far as lines of light appear along the dark bars. The colors of the panes are dim yellow and violet. When projected on a bright surface, as the sky, the after-image is negative. This result has been partially confirmed by a second observer, in whose case the after-image lasted three weeks, after which it could not be distinctly observed.[1]

The theory of Fechner and v. Helmholtz that positive after-images are due to persistence of motion in the retina and that negative and complementary after-images are due to exhaustion offers a rough-and-ready explanation of the more evident phenomena, but is inadequate in many ways. The recurrence of the positive after-image several times, as observed by Purkinje, Plateau, and Aubert, and by all the students of the writer, and its duration for many months in the observation given above, cannot be due to simple persistence of the original stimulation. According to v. Helmholtz, the color of negative after-images is due to exhaustion of the eye for the original color and the consequent preponderance of other colors when the eye is stimulated by white light. But this is contradicted by the great brilliancy of colors and the fact that they are seen best when all external light is excluded. The theory of Hering accounts better for the facts, and is more adequate from the point of view of psychology. But it is not easy to believe that a process of assimilation is accompanied by a sensation, especially one that differs only in quality from the accompanying process of dissimilation. Theories of color-vision have recently been elaborated by Wundt, Donders, Franklin, and Ebbinghaus, and it is certainly time to stop teaching the Young-Helmholtz theory in elementary text-books of physics and physiology. To

[1] Since writing the above I have read in a letter by Newton (Brewster's Life) a description of a persistent after-image of the sun.

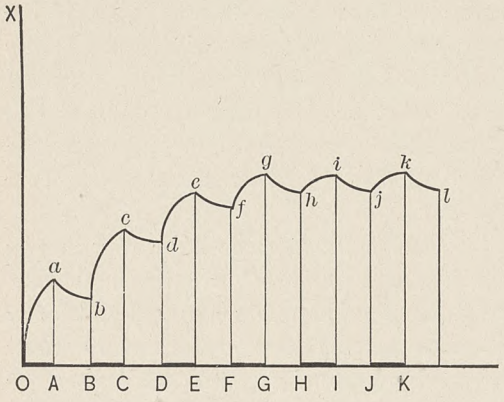
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the psychologist it is gratifying to know that the facts are obtained by introspection and psychological experiment, the physiological theories being based on these facts and not on any knowledge of processes in the eye and the brain. The psychological facts are established, whereas the physiological theories are in dispute.

XV.—INTERMITTENT STIMULATION.

One of the most important consequences of after-images and the inertia of the nervous mechanism is the fusion of stimuli which follow each other in rapid succession. Thus, in the case of the disks which have already been referred to and illustrated (Fig. 3) the sectors fuse and give a uniform sensation. The phenomenon can be illustrated by the accompanying figure. Suppose the eye to be stimulated by the lights *OA*, *BC*, *DE*, etc., there being alternate pauses *AB*, *CD*, *EF*, etc. Time is thus represented by the horizontal line, the abscissa (each subdivision being say 0.01 second), and intensity of sensation by the vertical lines (the ordinates), the light being such as would give an intensity of sensation *OX*. If there were no inertia of the visual mechanism, one would have for 0.01 second a sensation equal to *OX*, then for 0.01 second a complete absence of sensation, then another sensation for 0.01 second, etc. As a matter of fact, however, in the first 0.01 second the light only partly produces its effect (as explained in Section X.), and one has a sensation whose intensity is represented by *Aa*. Then when the light ceases for 0.01 second the motion of the visual mechanism does not subside entirely, but gradually, the sensation after 0.01 second being *Bb*. A new stimulation carries the sensation to *Cc*, which in the pause falls to *Dd*, and so on, until the amount of fall during each pause is equal to the amount of rise during each stimulation. If the times be longer than about 0.01 second, there will be a flickering sensation, the rise and fall of sensation being given in consciousness. If the times are shorter than about 0.01 second, the intermittent stimulation gives a uniform sensation. This would follow from the facts discussed under the perception of small differences (Section II.). If the time be so short that the fall in sensation is less than would occur were the light decreased by say one-hundredth of its amount, no difference will be perceived.

Fig. 15.



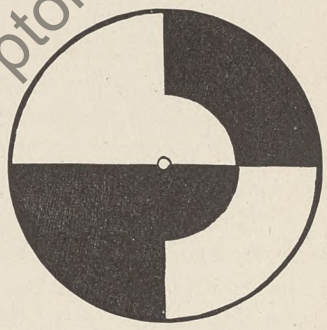
Alternate stimulations and pauses can be given most conveniently by

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means of revolving wheels. The pause can be secured by painting one-half or other sector of the wheel black, or (as all pigments reflect some light) the pause can be made complete by revolving a sector before a dark box. The intervals at which fusion occurs become longer as the light is taken fainter. This is probably due to the fact that the just perceptible difference is a larger part of a faint light. v. Helmholtz found that ten revolutions per second were sufficient to cause fusion in the light of the full moon, and twenty-four revolutions per second in strong lamplight. Others (Plateau, Aubert, and the present writer) find a more rapid rate of revolution necessary—about fifty per second—in ordinary diffused daylight, the duration of the stimulation and pause together being thus about 0.02 second. Ferry has found that the duration decreases from about 0.04 to about 0.02 second as the intensity of the light is increased twenty-four-fold, and deduces the law, "the duration of retinal impression is inversely proportional to the logarithm of the luminosity." Plateau and Emsmann found the period at which fusion occurs to be dependent on the color; but Ferry has shown that the difference in time is probably due to the varying intensities of the colors.

When complete fusion occurs, and the sensation is uniform, the intensity is the same as would occur were the same amount of light spread uniformly over the disk. This was first stated by Talbot (1834), and is known as Talbot's law. It has been verified experimentally by Plateau, Fick, and v. Helmholtz. After fusion occurs, increasing the rate of stimulation does not alter the intensity of illumination. This can readily be demonstrated by a disk such as is shown in the figure. When this is revolved fifty times per second, the inner circle, where there are fifty interruptions, and the outer circle, where there are one hundred interruptions, appear of the same intensity. Before the disk revolves rapidly enough to secure complete fusion it is brighter than when complete fusion occurs, the sensation having time to arrive at a maximum (cf. Section X.). Revolving wheels are one of the most convenient methods for measuring the intensity of lights and also for mingling colors. The fusion of spectrum colors has been studied by Nichols and Ferry, who revolved dark sectors before the colors, and spectrum colors could be mixed by means of revolving prisms or mirrors.

FIG. 16.



The fusion of sensation gives the impression of movement in the instrument (known as a toy) called the stroboscope, or "wheel of life." By various methods objects in the position they would have at intervals in the course of movements are shown successively, and the impressions fuse and give the appearance of natural movements. Lissajous's curves, showing

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the vibrations of tuning-forks, also depend on this principle. Conversely, in daily life an object in motion makes a total impression, and we are unable to distinguish the separate positions. Instantaneous photographs (as those by Muybridge) show the positions of animals when moving, and these are such as no one could have perceived by looking at the animal.

XVI.—THE REACTION-TIME ON LIGHT AND THE TIME OF PERCEPTION.

In treating the time-phenomena of vision we have so far considered the relation between the time of stimulation and the nature of sensation, and the continuation of sensation after the stimulation ceases. We should not, however, neglect the time required to convert the physical energy into a nervous impulse, the time required to transmit the nervous impulse along the optic nerve to the brain, and the time taken up in cerebral changes and in consciousness before the impression is perceived. These times have often been confused with the time threshold, the time of stimulation for maximum sensation, and with one another. Yet the processes are entirely different, and the times are not only different but independent. Thus, in a general way, the time a light must work on the retina in order to excite a sensation may be 0.001 second, the time it must work to call forth the maximum sensation may be 0.02 second, the impulse may travel along the optic nerve at the rate of sixty metres per second, and the time of perception may be 0.05 to 0.2 second. The first three times depend largely on the intensity of the light; the last time depends chiefly on the complexity of the impression, whereas the rate in the nerve is probably independent of either intensity or complexity.

Science has not succeeded in determining separately the times we are now considering, but a complex time which includes them may be measured with great accuracy. This is the *reaction-time*, the time elapsing after a light or other stimulus has occurred until a movement is made. The process requires 0.1 to 0.2 second. Its time, the factors of which it is composed, and its alterations under various conditions have been studied by many observers. The best general treatment of the subject is given by Jastrow[1] and Wundt.[2]

During the time of the reaction the light is converted into a nervous impulse, the impulse travels to the brain, in the brain changes occur which release a predetermined movement, the motor impulse travels (say) along the spinal cord and motor nerve to the hand, and the muscle is innervated. The time required to convert the light into a nervous impulse may be 0.02 second, varying, doubtless, with the intensity of the light. This time is, however, only an assumption from the facts of intermittent stimulation, already considered, and the fact that the reaction-time for light is longer than for the so-called mechanical senses, hearing and touch, with which this

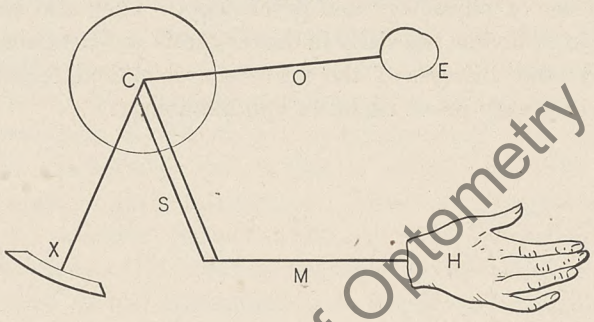
[1] The Time-Relations of Mental Phenomena, New York, 1890.
[2] Op. cit.

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time would almost disappear. The time of transmission along the sensory nerve has been studied (in the first instance by v. Helmholtz) by applying a stimulus to the skin nearer or farther away, and determining the difference in the length of the reaction-time, or by comparing the time at which the impressions arrive in consciousness. The difficulties in the way of such experiments are considerable, and the results of the numerous researches which have been made are not accordant. The rate of transmission in the motor nerve may be studied by directly stimulating the nerve-trunk at varying distances from the muscle and measuring the time elapsing before a contraction occurs. This can be managed more easily than experiments on sensory nerves, and the rates are commonly supposed to be the same in the two cases. This rate is said to be from thirty to sixty metres per second.[1]

It was formerly thought that the light was seen and a movement willed, but it is more likely that the "willing" is done beforehand, and consists in placing the centres concerned with the special movement in a state of unstable equilibrium. Then when the stimulus occurs the movement is discharged reflexly before we see the light and recognize its nature. This may be understood by reference to the accompanying figure. The light

FIG. 17.



strikes the eye (E), and after a certain time (taken up probably in chemical changes) an impulse is sent along the optic nerve (O) at a given rate. It reaches a brain-centre (C) which it finds in a state of unstable equilibrium. The impulse is now divided, changes proceed to the cortex (X), where the nature of the light is distinguished, and simultaneously other changes proceed from the centre along the spinal cord (S) and motor nerve (M) to the hand, where innervation takes place. The time of the reflex act of blinking is, according to Exner, about 0.06 second.

The length of the reaction varies with the intensity and area of the light, but the color has no appreciable effect. It also varies with the attention, fatigue, etc., of the observer. It is this latter fact which is of especial interest to the physician. The variation in length and regularity of the

[1] Charles S. Dolley and J. McK. Cattell, On Reaction-Times and the Velocity of the Nervous Impulse, Psych. Rev., vol. i. No. 11, March, 1894, pp. 159–168.

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reaction depends on the condition of the eye and other parts of the visual mechanism, and the relations deserve careful study, as they add to the accuracy and range of methods of diagnosis.

The time required to perceive the nature of an impression may also be determined. Thus conditions may be arranged so that the impression must be distinguished before the movement is made. The observer, for example, does not know what color will be presented, and is told to move his hand only in case blue occur. In this case the movement cannot be released until the nature of the impression is distinguished, although here, too, the co-ordination of the movement with the impression may be substantially automatic. The writer found the time required to distinguish a white light to be about 0.05 second, a color from other colors 0.10, the picture of an object 0.11, a letter 0.12, a word 0.13 second. It is also possible to measure the time of movements in answer to visual impressions: thus, it takes about 0.4 second to name a word and about 0.6 second to name a color. The difference in time is due to our greater practice in reading, and does not hold for the uneducated. We can also determine the time of processes which we know only on the side of consciousness, such as judging which of two lights is the brighter or the time required for one idea to suggest another. Such determinations are important, as they make an exact science of physiology and psychology. They also have practical applications in medicine, especially in the diagnosis and treatment of aphasia, insanity, and other diseases of the nervous system, and there is reason to believe that they may prove useful in ophthalmology.

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BINOCULAR VISION, CONFLICT OF THE FIELDS OF VISION, APPARENT AND NATURAL SIZE OF OBJECTS, ETC.[1]

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I. INTRODUCTION: PERCEPTION OF DEPTH IN MONOCULAR VISION.

THE human eye is like a photographic apparatus, the lens corresponding to the objective and the retina to the receiving plate. As the photographic image is only a superficial projection of the space pictured, so also the excitations caused by light upon the retina are arranged in a two-dimensional order, and it would therefore seem natural that we should have considered them as related to a two-dimensional form in the outer world. Every one, however, knows that we immediately refer our visual sensations to space of three dimensions. Every concept got through the sense of sight is a spatial concept. The objects which our visual sensations appear to give us cognizance of are, even when we look at them with one eye, perceived as not only extension in height and breadth, as corresponds to the structure of the eye, but also as extension in depth: that is, in addition to height and breadth, we have a clear conception that the objects we look at are at different distances from the eye of the observer. This perception of depth is, indeed, less perfectly developed than the perception of the other two dimensions: the painter of pictures and of panoramas is highly successful in deceiving the eye and in conveying the impression of a scene in space when in reality nothing but a surface is

[1] Upon account of the limits of space, only a few references are given to the literature of the subject. A full bibliography up to 1866 will be found in the first edition of Helmholtz's Physiologische Optik. In the new edition of this work there will be a complete bibliography coming down to the present time, prepared by Professor A. König. The chapters in Helmholtz's book in which this subject is discussed will be a simple reprint of the first edition. Since in this second edition the paging of the first is reproduced, references will here be made to the first edition. Among other exhaustive discussions of the subject here treated may be mentioned "Der Raumsinn und die Bewegungen des Auges," by Hering, in Herrmann's "Handbuch der Physiologie."

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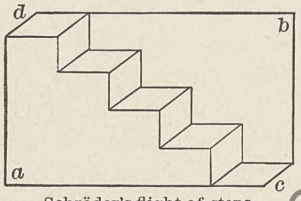
presented to the eye, though this impression remains less strong than that of an extended surface.

When we analyze the various means by which the idea of depth—*i.e.*, of varying distances of objects from the beholder—is attained, we find that they fall naturally into two classes. The first is the class of those which arise from experience; in these the feeling of depth is not given directly as a sensation, but is obtained as an inference from other sensations. It is by means of this class that the painter produces the plastic effect of his pictures.

To accomplish this the eye has to compare objects in respect to their size, and added to this is the experience which we have stored up in regard to the relative sizes of known objects. The size of an object in sensation —that is, the size of its image upon the retina—depends upon the visual angle under which it is seen. When, therefore, objects which we know to be of the same size give images of different sizes, we attribute to them a factor of greater distance in proportion as they are seen to be smaller. Thus the apparent size of some men on a tower, or on a distant country road, gives us information as to the remoteness of the tower or of the road. It is such well-known objects of definite size that the painter makes use of as accessories in order to give to the beholder a distinct impression of the relative distances of all the objects that are represented in his painting.[1]

Objects of relatively simple geometrical forms (houses, rooms, streets), which we know exactly from having constantly seen them from all sides, produce at the first glance an impression of solidity; and it is comparatively easy, in drawings of such objects, provided that they are executed with anything like a correct perspective, to convey at once the feeling of their existence in space. Very instructive in this respect is the Schröder flight of steps.[2] (Fig. 1.) The picture produces at once the impression of a flight of steps against a wall, beginning at the right and ending at the left, this being so whether one looks at it with the line *ac* below, or, after turning it through an angle of 180°, with the line *bd* below. If the first impression be kept distinctly in mind while turning the picture upside down, an overhanging, stair-like piece of masonry leaning against a wall will be seen. If now the first impression be recalled to mind, the object looked at will be suddenly transformed into a flight of steps beginning at *d*. Moreover, while before the impression predominated that the surface *a* was

FIG. 1.



Schröder's flight of steps.

[1] The extreme importance of this means for the perception of varying depth is evidenced by the fact that mountain-climbers, especially in barren and snow-covered regions, find it impossible to estimate distances correctly. (See Bonvalot's "Across Thibet.") "Here, in a few weeks, we have lost the sense of distance which we had gained by the experience of our lifetime."—TRANS.

[2] Helmholtz, Physiologische Optik, and Pogg. Ann., cv. S. 298.

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the nearer to the eye, the surface *b* will now appear the nearer. After some practice, either impression can be produced at will.

Of great importance for the perception of depth is the distribution of light and shade in the field of view,—not only in regard to the shadows that are cast by objects, but also in reference to the different degrees of illumination according as objects are turned towards or away from the source of light. That a well-shaded picture gives a far better impression of depth than one that is not shaded is well known.

Again, the so-called aerial perspective is of great importance in determining the feeling of space. The atmosphere is always more or less full of vapor and of cloud, and distant objects, therefore, have more or less the appearance of being veiled. Hence we easily believe the same mountains when they are misty to be nearer, and therefore larger, than when they are seen in a clear, transparent light. For the same reason the moon and the sun when they are near the horizon and their rays consequently pass through a greater thickness of atmosphere appear to us to be larger than when they are near the zenith.[1] They appear to be especially large in a misty atmosphere.

The second division of means by which we judge of distance depends directly upon sensation. The least essential is the feeling of change of accommodation. If, in the monocular vision of objects not very far away, we direct the attention from a more distant to a nearer object, we have plainly the feeling of the muscular effort involved. This gives a means, which is, to be sure, very uncertain, for the estimation of the relative distance of two objects. Wundt[2] has made experiments upon this subject by means of a stretched thread whose ends were not visible, and which could be made to approach or to recede from the eye, and also by means of two such threads. He came to the conclusion that the feeling of accommodation gives no information in regard to the absolute distance of an object, but only in regard to its relative distance, and that the less the absolute distance the more certain is the estimation of relative distance. For a distance of forty centimetres between the eye and the thread, for instance, the limit of perceptible change is four and one-half centimetres. In general, the latter

[1] The reason just given is certainly at least the principal one for this phenomenon. It has, indeed, been affirmed that the moon and the sun appear larger in the horizon even when the atmosphere is perfectly clear. According to Smith (1755), this is due to the fact that the vault of heaven does not appear to us to be in the form of a hemisphere, but in that of a flatter vaulted surface, about the shape of a watch-glass. The moon in the zenith, therefore, seems to us to be nearer, and since we see it under the same visual angle we take it to be larger. Helmholtz, by means of a glass plate with plane parallel surfaces, used as a mirror, threw an image of the moon in the zenith upon the horizon, and failed to detect any distinct change in its size. On the other hand, direct experiments which Strobant (1884) carried out in a room, in which he compared the apparent distance of bright points on the ceiling and at an equal distance from the observer on the wall, gave the result that those on the wall appeared to be farther away.

[2] Theorie der Sinneswahrnehmungen.

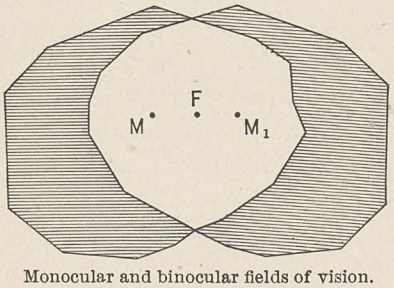
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quantity is less; that is, the capacity for forming a judgment is greater when the thread is moved farther away than when it is brought nearer.

Further, we are able to form a judgment as to the different distances of objects from one another by means of a change in the retinal images produced by motion,—not only the motion of the objects relatively to each other, but also, and especially, the motion of the observer. When the eye is moved, the images of objects change their relative position upon the retina, the images of the more distant objects moving less rapidly, and those of very distant objects (*e.g.*, the stars) not moving at all. This change in the images produces a feeling of space; and when, in paintings and especially in panoramas, a plastic impression has been produced, the observer must not change his position, or he will lose this impression for the moment. We make use of this power of motion in the eye, in scientific experiments, to bring an optical image into coincidence with some object (for example, the crossed threads of a telescope).

When we fix our eyes upon any object, the greater part of the objects which we see at the same time throw an image upon both retinas. It is true, however, that not the whole field of vision is seen binocularly, the outer part on one or the other side being seen with the eye of that side only. A very considerable increase of the field of vision is secured by this monocular part. According to Aubert,[1] the field of vision in the horizontal meridian, with the eye at rest, for one eye, includes 145°,—55° inward from the point of fixation and 90° outward: the binocular field, therefore, amounts to 180°. It is plain that the increase from 145° to 180° is of great importance for the certainty of our motions in space. Fig. 2 gives a representation of the field of vision according to Möser.[2] The monocular part is shaded, F is the fixation-point, and M and M_1 are the blind spots. The middle unshaded part corresponds to that portion of the field of vision which is seen binocularly.

FIG. 2.



Monocular and binocular fields of vision.

II. PERCEPTION OF DEPTH BY MEANS OF BINOCULAR VISION; STEREOSCOPIC VISION.

When we look at an object with two eyes, the two retinas do not both receive exactly the same image, for the two eyes have a slightly different position in space. If we look at a folded sheet of paper held so that the folded edge is in the median plane (the plane perpendicular to the line joining the nodal points of the two eyes at its middle point), we see, when we shut the left eye, more of the right half of the sheet of paper; when we

[1] Physiologische Optik.

[2] Das Perimeter und seine Andeutung.

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shut the right eye, we see more of the left half. We have not, however, commonly, when we look with two eyes, the sensation that we are seeing double. On the contrary, the effect of the images upon the two retinas is to produce a definite idea of space, especially for near objects. When we look with one eye at an object which is unfamiliar to us, and which has irregular bounding surfaces (as a roughly broken stone), we have only a very indefinite impression as to the arrangement of the bounding surfaces, but they become immediately plain to us as soon as we look at it with both eyes.

When we consider stereoscopic pictures we recognize very plainly the influence of vision with two eyes upon the perception of depth. If we make two perspective drawings of some simple regular solid body,—a cube, for instance,—one from the point of view of the right eye, the other from that of the left eye, and if we look at these two drawings, one with the right eye and the other with the left eye, in such a way that the two retinal images fall upon exactly the same parts of the retinas (as they would do in the case of a real solid body), we have immediately, and with great clearness, the impression of a solid body. Such pictures are called stereoscopic pictures, and after some practice one can look at them in the proper way. They should be placed at a distance apart that is equal to the distance between the eyes, and in such a way that corresponding points are at the same height, and then looked at with the axes of the eyes parallel. This is not easy at first, because one is accustomed to accommodate for a distant point and not for a near one when the axes of the eyes are parallel. When this is accomplished, one sees three images, two with each eye, of which the two middle ones, by fusion with each other, give rise to the impression of a solid body.

FIG. 3.

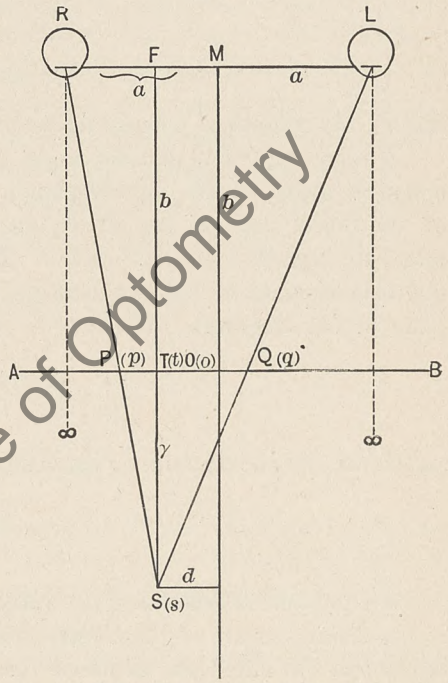


Diagram to explain stereoscopic vision.

Stereoscopic pictures may be made either by geometrical construction or by photography, which latter gives, of course, a central projection. If in Fig. 3 R and L are supposed to be the nodal points of the two eyes, and M the middle point of the line joining them, and if, further, MO is a horizontal perpendicular to RL, of the length of distinct vision, and AB is the projection of a plane through O and perpendicular to OM,

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then the plane AB is the plane of the picture, and to every point of the space to be represented, as S (which does not in general, of course, lie in the plane of the paper), lines must be drawn from each eye. If these lines meet the plane of the picture AB in the points P and Q respectively, then all points P form one stereoscopic picture and all points Q the other. If stereoscopic pictures are to be produced with exactness by photography, two impressions must be taken at distances apart that are equal to the average distance between the two eyes, and with objectives whose focal lengths are exactly alike and about equal to the distance of distinct vision.

We add some rules of stereoscopic representation.[1] Let a perpendicular SF fall from S, in Fig. 3, upon the line RL, cutting the plane of the picture in T, and at the points P, Q, T, S let fall perpendiculars upon the horizontal plane Pp, Qq, Tt, Ss.[2] Let the distance between the eyes RL be represented by Qa, the distance of distinct vision by b, the distance of the object S from the plane of the picture by γ, and, finally, put FM equal to α.

Then

$$\frac{Ss}{Pp} = \frac{SR}{PR}, \text{ and } \frac{Ss}{Qq} = \frac{SL}{QL};$$

and therefore, since

$$\frac{SR}{PR} = \frac{SL}{QL},$$

$$Pp = Qq = v;$$

that is, the heights of corresponding points of the two pictures are equal.

We have also PQ parallel to pq, and therefore $PQ = pq$; that is, the distances apart, on the picture-plane, of the images of (1) a given point of the object and (2) the projection of that point upon the horizontal plane through the eyes, are equal. Therefore it is sufficient to determine the distance apart of the two images of a point in this horizontal plane (the plane of the diagram). We have

$$\frac{pq}{Qa} = \frac{ps}{RS} = \frac{st}{sF} = \frac{\gamma}{\gamma + b},$$

and hence, for the distance in question,

$$pq = \frac{Qa\gamma}{\gamma + b}.$$

We proceed to determine the value of the stereoscopic parallax,—that is, the distance apart of the corresponding points of two stereoscopic drawings when the latter are so placed that the images of an object at infinity coincide. In our figure the images of an infinitely distant object do not coincide, but are at a distance apart; that is, they are equal to the distance between the two eyes, or Qa. The stereoscopic parallax is obtained, there-

[1] For further details see Helmholtz, Physiologische Optik, p. 664 ff.

[2] In the diagram the feet of the perpendiculars are enclosed in parentheses.

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fore, by subtracting from Qa the distance apart of the two images of an arbitrary point; thus,

$$e = Qa - \frac{Qa\gamma}{\gamma + b} = \frac{Qab}{b + \gamma},$$

or, if we write ρ for $b + \gamma$,—that is, for the distance between the point of the object S and a vertical plane through the nodal points of the eyes,—

$$e = \frac{Qab}{\rho}.$$

Since Qa and b are constants, it follows that *the stereoscopic parallax depends only upon the distance between a point of the object and the vertical plane through the nodal points of the eyes, and is inversely proportional to this distance.*

This circumstance, that the stereoscopic parallax is the same for all objects equally far away, has been utilized by O. N. Rood in the construction of an apparatus by means of which for every perspective drawing the corresponding stereoscopic drawing can readily be produced. It consists of a frame which is movable in one direction (the direction of the stereoscopic parallax), the amount of motion being capable of being measured. In this framework is fastened a piece of transparent paper, and underneath is the original picture, which is to be drawn through, but in such a way that with a given position of the frame all those points are to be drawn which are in a given plane of the picture. On passing to another plane of the picture the frame is to be shoved on by a corresponding amount.

Let the amount of the parallax belonging to two different distances of the object ρ_1 and ρ_2 be e_1 and e_2 respectively; then we have

$$e_1 - e_2 = Qab\left(\frac{1}{\rho_1} - \frac{1}{\rho_2}\right);$$

or, if we put

$$\rho_1 \rho_2 = n^2,$$

then

$$\rho_2 - \rho_1 = n^2 \frac{e_1 - e_2}{Qab}.$$

If in this formula $e_1 - e_2$ represents the least difference in distance which is stereoscopically perceptible, then we have expressed the fact that *the differences in depth which are stereoscopically just perceptible vary directly as the square of the mean distance of the points.*

Helmholtz has made experiments to determine with what exactness differences in the two retinal images can be detected, and he has found that a difference of one minute of arc is sufficient to be perceived.[1] It should be noticed, in passing, that this is about the same angular distance as that at which two bright points can be distinguished as two. If we now put in

[1] Physiologische Optik, p. 644.

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the above formula $\rho_2 = \omega$, and call ε the angle at which, in stereoscopic vision, one point is seen to be just perceptibly behind another, we have

$$\rho_1 = \frac{Qab}{e_1 - e_2} = \frac{Qa}{\sin \varepsilon}.$$

The distance apart of the eyes as thus estimated is sixty-eight millimetres (Helmholtz): hence

$$\rho_1 = \frac{68}{\sin 1'} = \text{(about) } 240 \text{ metres.}$$

The greatest distance, therefore, at which one can obtain stereoscopic effects is two hundred and forty metres. It is hence of no use for stereoscopic purposes to take photographs of objects more than two hundred and forty metres away, if the distance between the objectives is the same as the distance between the eyes.

A visual angle of one minute corresponds, at the distance of distinct vision, to not quite one-tenth of a millimetre of length. If, therefore, there are two drawings which are nearly alike, but which differ from each other in any part by so much as one-tenth of a millimetre, this difference will be at once apparent if they are looked at stereoscopically. According to Dove, this method is made use of to detect counterfeit paper money; differences can be determined between impressions which are not made from the same die, though they look exactly alike when compared in the ordinary way.[1] We do not need to mention that the difference to be detected does not consist in an appearance of indistinctness, as would be the case if one picture were superimposed upon the other by optical means and they were then looked at with one eye: what happens is that the irregular parts of the picture seem to be in a different antero-posterior plane.

We shall now determine how, in looking at stereoscopic pictures, the apparent position of an object depends upon the position of its images. The apparent position of the object is determined by ρ, by $Ss = \beta$, and by $FM = a$. By a former equation we have

$$\rho = x + b = b\,\frac{Qa}{e},$$

and also

$$\frac{\beta}{v} = \frac{\rho}{b} = \frac{Qa}{e},$$

and hence

$$\beta = v\,\frac{Qa}{e}.$$

Finally,

$$\frac{\rho}{b} = \frac{a - a}{tp}, \text{ or } tp = \frac{b}{\rho}(a - a),$$

and

$$\frac{\rho}{b} = \frac{a + a}{tq}, \text{ or } tq = \frac{b}{\rho}(a + a);$$

[1] Hirth, Das plastische Sehen, German and French editions, contains a number of interesting stereoscopic objects.

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hence

$$tq - tp = \frac{b}{\rho} Qa;$$

or, since

$$qo - op = \frac{e}{a} a,$$

$$a = (qo - op)\frac{a}{e}.$$

If we put $\frac{qo - op}{Q} = x$, where x is the arithmetical mean of the distances of two corresponding points of the image from the median plane, we have

$$a = x\frac{Qa}{e}.$$

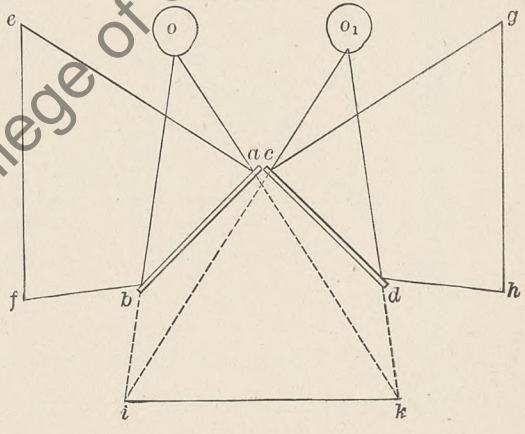
If, then, two stereoscopic pictures, drawn according to the plan represented in Fig. 3, are brought nearer to the eye or are removed farther from the eye, b becomes respectively smaller or larger; β and α are not changed, but ρ becomes smaller or larger proportionately with b; that is, in the first case the depth of the apparent object is too small, in the second it is too great. This occurs when photographic stereoscopic pictures are looked at at a distance that is not equal to the distance between the photographic plate and the focus of the objective which lies nearest to it.

III. STEREOSCOPIC APPARATUS.

To look at stereoscopic pictures with the axes of the eyes parallel requires a certain amount of practice. For the sake of greater convenience, apparatus has been devised by means of which the stereoscopic effect can be produced with the axes of the eyes convergent. The earliest of these instruments is:

(*a*) *The Mirror-Stereoscope of Wheatstone* (*invented in 1833*).—It consists, as is shown in Fig. 4 schematically, of two mirrors that are inclined to each other at an angle of 90°, *ab* and *cd*; *o*, o_1, are the positions of the two eyes, *ef* and *gh* of the two stereoscopic views. The mirrors form virtual images of these views, which fall exactly together in *ik*, and of which one is seen with one eye and the other with the other eye. The distance of the virtual images from the eye must be that of distinct vision.

FIG. 4.

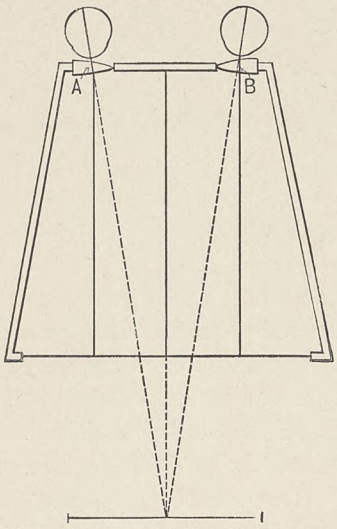


(*b*) *The Lens-Stereoscope of Brewster* (*1843*).—This instrument has the advantage that it is far more handy than Wheatstone's, that the pictures lie side by side and so can be fixed upon a single piece of

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card-board, and that a good illumination can be more readily obtained. This is the form of stereoscope that is found in common use. The arrangement is schematically represented in Fig. 5. *A* and *B* are two prismatic lenses, which are so chosen that by means of the prismatic deviation, upon convergence for the distance of distinct vision, two pictures which are as far apart as the distance between the eyes are seen single, while, by reason of the lenses, the pictures, which are usually nearer than for distinct vision, are seen distinctly; thus a slight enlargement of the pictures is obtained at the same time. In order to obtain a perfect effect, the photographic pictures must have been properly taken; this, however, is seldom the case. Moreover, there is the disadvantage that the pictures, especially on the edges, show some color, unless achromatic prisms have been chosen, which also is seldom done.

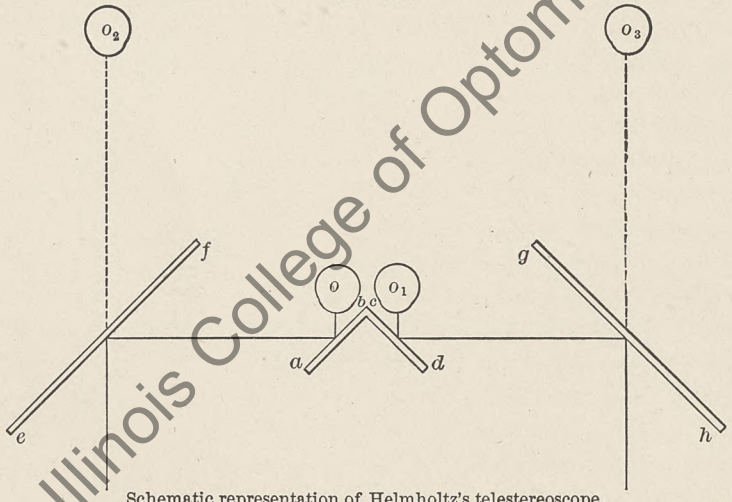
FIG. 5.



Schematic representation of the lens-stereoscope of Brewster.

(*c*) *Helmholtz's Stereoscope.*—Since, in the stereoscopic views to be found in the shops, corresponding points are often not at exactly the right distance apart, and the heights are also sometimes not exactly the same, Helmholtz has constructed a stereoscope in which both

FIG. 6.



Schematic representation of Helmholtz's telestereoscope.

of these faults can be corrected. This instrument is designed to be used with accommodation for infinity and with the axes of the eyes parallel; the prisms, with their disadvantages, are therefore left out. Distinctness and, if it is desired, enlargement of the pictures are obtained by means of a

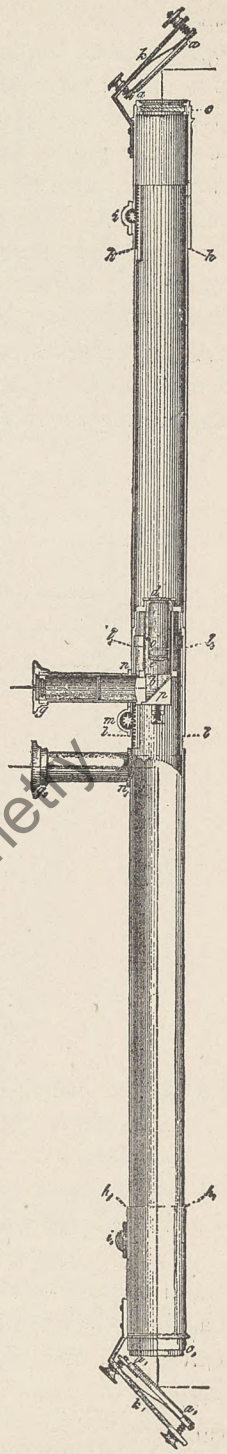
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combination of two convex lenses which can be brought nearer together or removed farther apart. Each pair of lenses can be moved, by means of two screws, in the direction of and at right angles with the line joining the eyes. It has the same external appearance as that of Brewster. Several other instruments of a similar kind have been constructed.

(*d*) *Helmholtz's Telestereoscope.*—We have seen that for a distance greater than two hundred and forty metres, with the ordinary distance between the eyes, a plastic effect cannot be obtained, upon account of the difference between the two retinal images. In order to bring out more clearly the dimension of depth for greater distances, Helmholtz has constructed the so-called *telestereoscope*, which is schematically represented in Fig. 6. The position of the two eyes is represented by o and o_1; *ab*, *cd*, *ef*, *gh*, are four plane mirrors which are at an angle of 45° with the median plane (*i.e.*, the plane perpendicular to the line joining the nodal points of the eyes at its middle point) in a way which is made plain by the figure. The effect of the mirrors is such that the apparent position of the eyes is at o_2 and o_3, or the effective distance between the eyes is increased. The apparent size of objects is not altered by this arrangement: it is as if one regarded an accurately reproduced model of a real scene, made smaller in the proportion of the actual to the apparent distance between the eyes, but at a correspondingly less distance. Exactly the same effect is produced by stereoscopic photographs if they are taken at distances apart greater than the distance between the eyes.

Helmholtz has combined this arrangement with two terrestrial telescopes by putting two rectangular prisms between the second and third lens of the objective and two plane mirrors behind the objective. The instrument is represented in Fig. 7. The mirrors *aa* and a_1a_1, which must be accurately constructed, can be so adjusted by screws that the images of the two telescopes fall exactly together for the observer. Helmholtz made use of a sixfold magnifying power, and of an apparent distance sixteen times greater than the actual distance. He therefore obtained the effect of a scene at a distance from the observer equal to one-sixteenth of the actual distance.

FIG. 7.



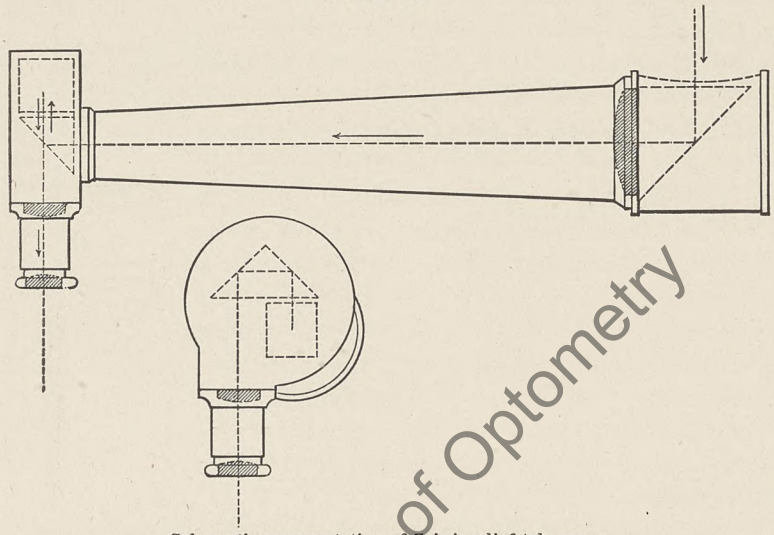
Helmholtz's telestereoscope.

(*e*) *Zeiss's Relief Telescope.*—The instrument just

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described did not come into common use, but Zeiss, of Jena, has recently taken up the idea. As is well known, the ordinary binocular telescopes (opera-glasses, field-glasses), which consist of two so-called Dutch telescopes, give only a very feeble enlargement, or if the magnifying power is made greater the field is extremely small. With a four- to sixfold magnifying power the field is only a third of the actual field. The terrestrial telescope cannot be used for this purpose, on account of its length and consequent unhandiness. The astronomical telescopes are shorter, but they are still too long, and, moreover, they give inverted images. Zeiss has therefore constructed astronomical telescopes after the design of Porros, which produce upright images by means of reflecting prisms, and combined them with binocular instruments. The totally reflecting prisms, whose construction we cannot further describe here, give opportunity for combining a telestereoscopic with the binocular effect. He makes both telestereoscopic

FIG. 8.



Schematic representation of Zeiss's relief telescope.

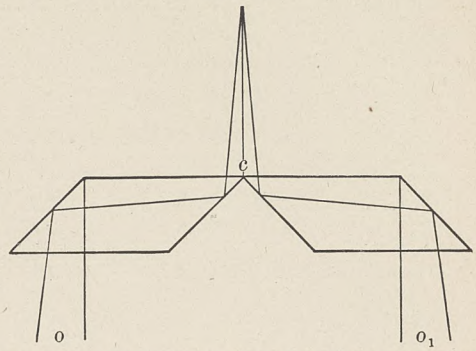
field-glasses, which have only a slight telestereoscopic effect, and relief telescopes, in which the apparent distance between the eyes is equal to twice the focal length of the objective. In Fig. 8 is shown, in two sections, one-half of the latter instrument,—the half intended for the right eye; *a* is a horizontal and *b* is a vertical section through the optic axis.

(*f*) *The Binocular Ophthalmoscope and Otoscope.*—It is sometimes desirable to produce the opposite effect to that obtained by the telestereoscope. This happens when it is desired to look at objects which one cannot see with both eyes at once because the distance between the eyes is too great, as, for example, the drum of the ear and the fundus of the eye. In this case we can make use of an instrument the essential part of which is represented in cross-section in Fig. 9. There are two glass prisms whose cross-section is

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a parallelogram with an acute angle of 45° ; two of their sharp edges come together in c, and o and o_1 indicate the position of the eyes of the observer. The rays which come from the object looked at are divided into two halves, one of which reaches the right eye and the other the left eye. They have a slight inclination towards each other. By this means is obtained a feeble but not unimportant stereoscopic effect. These instruments are constructed by Géraud-Teulon and by Bottcher.

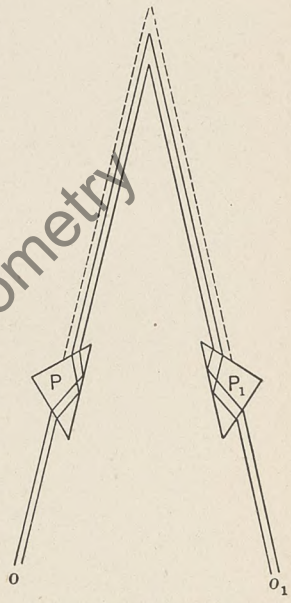
FIG. 9.



Schematic representation of binocular ophthalmoscope.

(*g*) *Wheatstone's Pseudoscope.*—This instrument is designed for the inversion of the relief of a natural object. It is instructive, as by its use stereoscopic vision may be set in opposition with the other means of plastic vision. In Fig. 10, P and P_1 represent the two prisms of this instrument, and o and o_1 the position of the eyes. Since total reflection takes place from the widest surface of these prisms, they have the effect of interchanging right and left without changing the direction of vision. By bringing two images into superposition the relief must appear inverted. The illusion does not always succeed, however; the other aids for the production of the dimension of depth, especially shadows, frequently destroy the expected result. Helmholtz recommends that objects which are to be seen pseudoscopically should be hung in the middle of a room with a monochrome background on which no shadows can be thrown. Wooden cylinders look like hollow tubes, and cigars appear like hollow sheets of tobacco. Righi, in 1889, described an apparatus which one can use both as pseudoscope and as telestereoscope. It consists of two parallel mirrors inclined at an angle of 45° to the median plane; that is, it is one-half of a Helmholtz mirror-telestereoscope. It is held before one eye only, while the other looks in the ordinary way. When held in the same way as the Helmholtz instrument, a telestereoscopic effect is produced. When the instrument is turned 180° about the axis of vision, the effect is pseudoscopic.

FIG. 10.



Schematic representation of Wheatstone's pseudoscope.

(*h*) *The Stereoscopic Microscope.*—This is a microscope with one objective and two eye-pieces. The rays which proceed from the object are

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divided into two halves, which are directed into two tubes by means of prisms. Such microscopes have been constructed by Nachet and by Wenham. Fig. 11 shows an arrangement of this sort. By means of three equilateral prisms, a, b, and c, of which one, a, is immediately over the objective d, there is produced a twofold total reflection and inversion of the rays. Another arrangement is exhibited in Fig. 12; the same result is here accomplished by two totally reflecting prisms, a and b. The prism a receives the right half of the rays which have come through the objective d, and, after reflection from the second prism, these rays reach the left eye of the observer. A screw is sometimes introduced, by means of which the prism a can be moved over the other half of the objective: a pseudoscopic effect is then produced. Abbe has constructed an eye-piece for the produc-

FIG. 11.

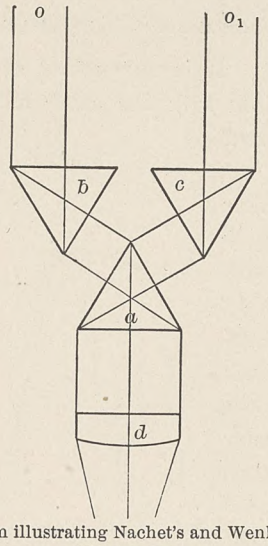


Diagram illustrating Nachet's and Wenham's microscopes.

FIG. 12.

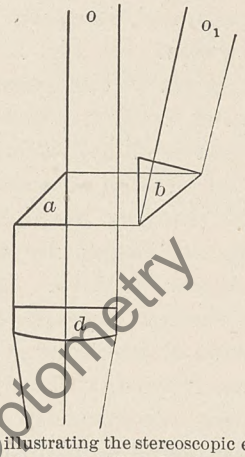


Diagram illustrating the stereoscopic effect obtained by two totally reflecting prisms.

tion of the stereoscopic effect with a microscope made for monocular use, which can be attached at once in place of an ordinary eye-piece.

It is to be remarked that in the microscopes just described the stereoscopic effect, as Helmholtz has shown, is brought about in a peculiar way, as the result of the circle of diffusion. Let a in Fig. 13 be a point of an object in the plane of accommodation PQ, and b a point somewhat below a. A sharp image of the plane PQ is formed for the right eye at $P'Q'$ by means of the objective; the image of a is therefore at a'. The image b of b_1 is then beneath the plane $P'Q'$, and in this plane there is a diffusion circle formed by b, of which, however, upon account of the shutting off of half the lens, only the right half is visible to the right eye. The centre, b_2, of this half diffusion circle, which represents for this eye the image of b, is therefore somewhat to the right of a'. In the same way, for the left eye, the image of b is to the left of a'. In the plane $P'Q'$ there is

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produced, therefore, in effect, for the two eyes taken together, a correct stereoscopic image of the point *b*.

IV. CORRESPONDING POINTS OF THE RETINA.

We have hitherto discussed the influence which binocular vision has upon the perception of depth in the visual space by a consideration of the total effect obtained, without analyzing in detail the unitary impression that is produced in spite of the fact that we see with two eyes and from two different positions. We shall now take up this latter problem. If we gaze at an object binocularly, and then push one eye a little to one side by the finger, we shall see two images of the object. From this it follows that it is not a matter of indifference, for the attainment of a single image, upon what portion of the retina the object is pictured; on the contrary, if the object is pictured for one eye on the position *a* of the retina, it must be pictured for the other eye on a perfectly definite position, *b*, of its retina, in order to secure coincidence. Portions of the two retinas which work together in this way are known as *corresponding points* (or *identical points*), and portions which have not this property are called *disparate points; different points* will refer, then, to different points on a single retina. From the fact that we see objects single which we gaze upon, it follows that the middle points of the fovea are corresponding points. If, in fixing our eyes upon an object that is situated in the median plane, we direct the attention upon an object that is considerably nearer or farther off than the object gazed at, we see that object not single, but double; as we say, there are double images. These images, therefore, fall upon disparate portions of the retinas.

FIG. 13.

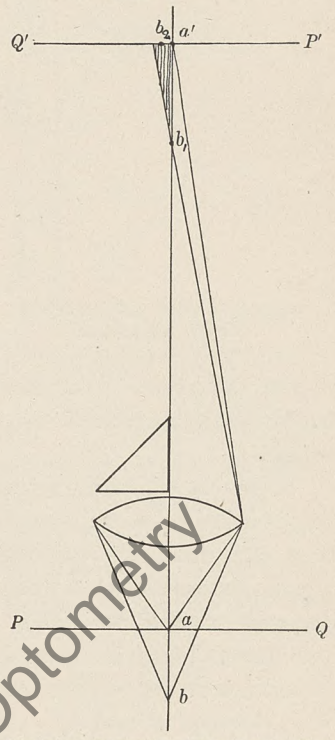


Diagram illustrating stereoscopic effect produced in binocular microscope.

For the further determination of corresponding points several different methods have been employed, some of which are fatiguing to the eye and some are applicable only in a limited region. The best method consists in the use of an apparatus which offers a special field of vision to each eye, while the contents of these two fields of vision are united in consciousness. Such an arrangement has been called by Hering a *haploscope*. For the following experiments it is sufficient if the instrument consists of a vertical screen upon which, at a horizontal distance apart that is equal to the distance between the eyes, two points are marked, as, for example, *f* and

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f' in Fig. 14. One is to look at this screen with both body and head held upright (the primary position) and with the visual lines (the lines which connect the nodal points of the eyes with their visual centres) placed horizontal and parallel. The left eye is to be directed upon the left mark f, and the right eye is to be fixed upon the right mark f'. If now at f a vertical line be drawn upward and one at f' drawn downward, the experimenter will see (since f and f' throw their images upon corresponding points) a continuous line gg'. This line, however, is not in general, as one might expect, a straight line, but the two lines form an obtuse angle with each other. The inclination of the two lines can be measured if one of the two lines—say $f'g'$—is made movable about an axis, and if the amount of its rotation can be read off upon the arc of a circle. This line can then be turned until it appears to be the exact continuation of the other. If in this new position of $f'g'$ both lines should be produced beyond f and f' respectively, only a single straight line would be visible.

FIG. 14.

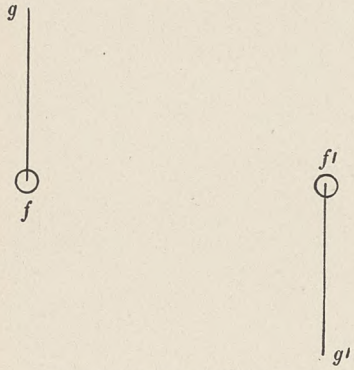


Diagram illustrating the action of Hering's haploscope.

A line in which the retina is cut by any plane going through the visual line is called a *retinal meridian*. From the above experiments it follows, then, that there are two retinal meridians, nearly but not exactly vertical, which correspond with each other. These are called by Helmholtz the *apparent vertical meridians*. Hering terms them the *longitudinal sections*, and Ruete designates them the *vertical lines of separation*. For most people these lines diverge above and converge below. The angle between them, V, is between 0° and 3°. In many cases the meridians seem not to form exactly straight lines, but appear to have a little indentation at the place of distinct vision.

FIG. 15.

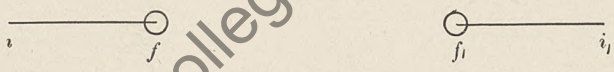


Diagram illustrating the action of Hering's haploscope.

If now one draws a line from f towards the left, fi, and a line from f' towards the right, $f'i'$, and observes as before, one will see either a straight line, ii' (Fig. 15), or an obtuse angle with its opening situated upward. According to Helmholtz, this line is straight for those who have normal vision, and forms an obtuse angle for those who are short-sighted. Even in the latter case, however, the departure from a straight line is far less than it is for the vertical lines (about $\frac{1}{2}$°). By rotating one line as before, the corresponding horizontal meridians can be obtained. These are called

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by Helmholtz the *retinal horizons*. Hering terms them *cross-sections*, and Ruete designates them the *horizontal divisional lines*.

Helmholtz and Donders have found that the angle V is not constant for any given observer. Hering attributes this to the fact that the eye involuntarily rolls slightly about the visual axis; if this is avoided, the angle remains constant. According to Hering, it can easily be brought about that the middle cross-sections coincide with the actual horizontal meridians by

FIG. 16.

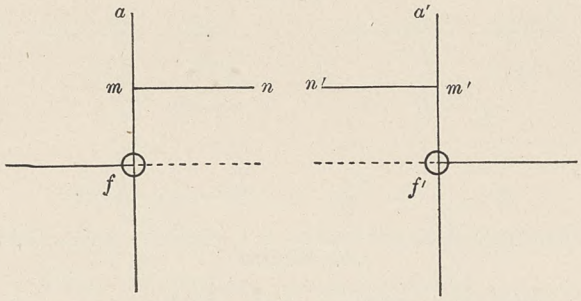


Diagram illustrating the method for determining corresponding points on the mean cross and longitudinal sections.

compelling the eyes, if necessary, to roll slightly. If one fixes the eyes in such a position by means of a horizontal thread which passes through the field of vision of both eyes, a constant value for V can be preserved.

We have now to investigate what points on the mean cross and longitudinal sections are corresponding points. To this end we introduce two rectangular (or nearly rectangular) crosses into the haploscope, with their

FIG. 17.

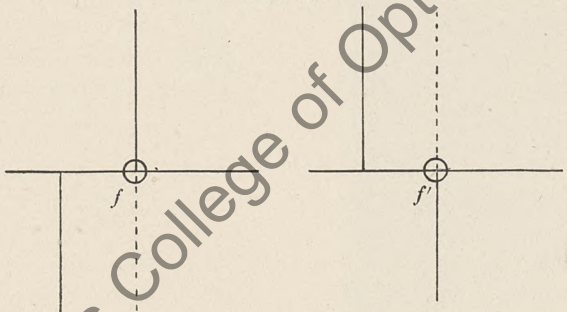


Diagram illustrating the method for determining corresponding points in the middle cross-sections.

intersections situated at f and f' and so placed that they will fall together in the visual field. (Fig. 16.) If then there are two horizontal lines mn and $m'n'$, which are movable up and down, and if one of them ($m'n'$) is moved until mn and $m'n'$ fall together in one straight line, it will be found that when this is the case the distances fm and $f'm'$ are equal. From this it follows that those points in the middle longitudinal section which are

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equally distant from the middle cross-section correspond.[1] By a similar arrangement, which is represented in Fig. 17, it will be found that in the

FIG. 18.

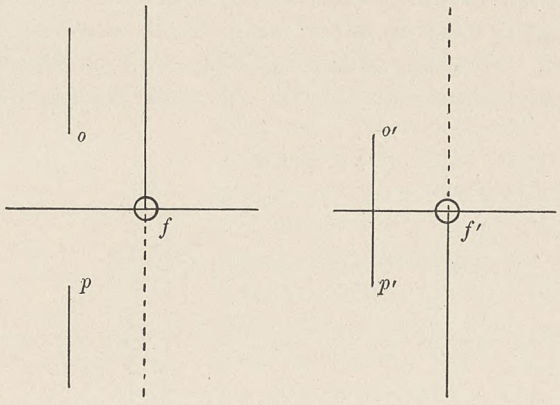


Diagram illustrating the method for determining corresponding points within any one of the quadrants.

middle cross-section those points correspond which are at equal distances from the middle longitudinal section.

Finally, to determine corresponding points within any one of the

FIG. 19.

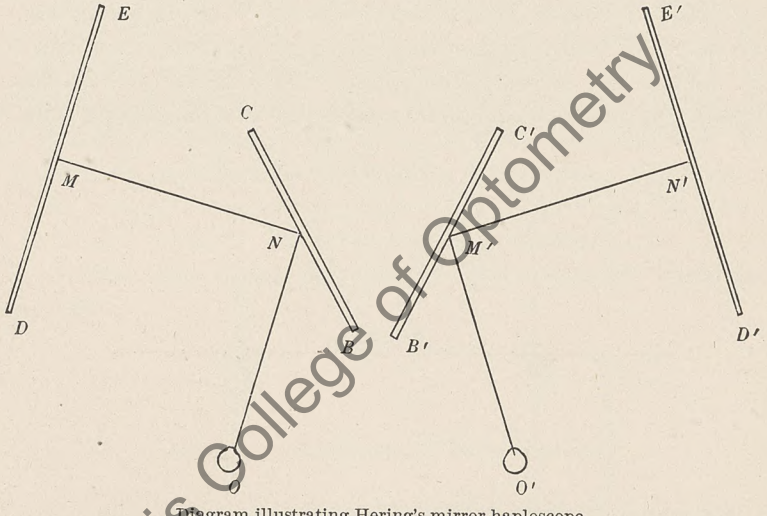


Diagram illustrating Hering's mirror-haploscope.

quadrants the haploscope should be arranged as in Fig. 18. If the points o and o', as well as the points p and p', are equally distant from both the

[1] It is still better if in these figures the dotted arm of the cross is omitted. The figures are drawn, for the sake of simplicity, for those eyes in which the middle longitudinal sections are not convergent. Let the reader compare what is said below about the fusion of double images.

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vertical and the horizontal lines through f and f', then in the haploscopic combination o will coincide with o' and p with p'. In order to carry out these and other haploscopic experiments with different degrees of convergence of the visual axes, the Hering *mirror-haploscope* may be employed. This is represented in Fig. 19. O and O' are the positions of the nodal points of the two eyes, BC and $B'C'$ are two mirrors, DE and $D'E'$ are the two haploscopic fields of vision, which are at an angle of 45° with the

FIG. 20.

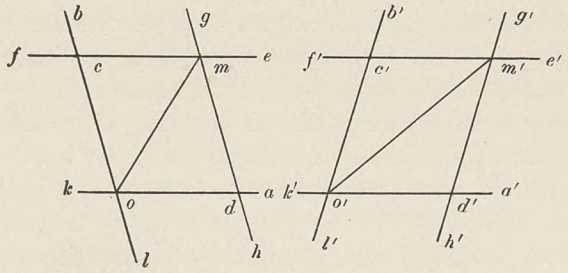
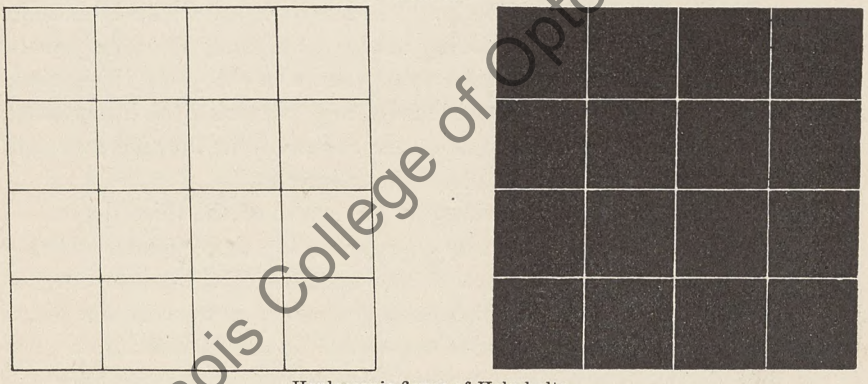


Diagram illustrating construction for finding corresponding points and corresponding meridians.

mirrors, and are so arranged that a ray of light perpendicular to each field at its middle point (MN and $M'N'$), after reflection from a mirror, reaches the nodal point of the corresponding eye (O and O'). To this end, BC, DE, and O on the one hand, and $B'C'$, $D'E'$, and O' on the other, are firmly connected together. Each of these systems, however, can be rotated about the points O and O' respectively, so that one is in a position to make the directions OMN and $O'M'N'$ correspond with every position of the

FIG. 21.



Haploscopic figure of Helmholtz.

visual axes. For a given position of the visual axes the apparatus is the same as the Wheatstone stereoscope.

In accordance with the foregoing propositions, all corresponding points and all corresponding meridians can easily be found by construction. With reference to the meridians, however, it must be remarked that, when meas-

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ured upon them, corresponding points are not equally distant from the visual centres in the case where the middle longitudinal sections are convergent. This is apparent from Fig. 20, where, for the sake of plainness, the convergence is exaggerated. If o and o' are the fixation-points, bl and $b'l'$ the middle longitudinal sections, and ak and $a'k'$ the middle cross-sections, then m and m' are corresponding points on the corresponding meridians om and $o'm'$. This is so, provided that $oc = o'c'$, $od = o'd'$, and $ef \parallel ak$, $e'f' \parallel a'k'$, $gh \parallel bl$, and $g'h' \parallel b'l'$. It is evident that om is not equal to $o'm'$. In performing these last experiments care must be taken that the lines be drawn increasingly thicker as they pass farther away from the centre. The reason for this is that the power of discriminating falls away very rapidly in the peripheral portions of the retina.

For the purpose of enabling this whole matter to be observed at once, Helmholtz has drawn the haploscopic figure which we have reproduced in Fig. 21. In order to avoid fusion when the lines do not fully correspond, the left half is drawn in black on white and the right in white on black. In haploscopic combination with parallel visual axes (if necessary, with a stereoscope) one sees two coincident rectangular gratings. For eyes which are not at this distance apart, or which have a different convergence of the apparent vertical meridians, a different picture must, of course, be drawn.

V. THE HOROPTER.

On the basis of the laws just given, we are in a position to determine for every position of the eyes what points in space will throw their images upon corresponding points of the retina. The entire collection of points which satisfy this condition is called the *horopter*. It is evident that, upon the doctrine of corresponding points already explained, the horopter can be determined mathematically. This problem has been solved by Helmholtz by analytical geometry, and by Hering at about the same time by synthetic geometry. We shall not undertake to reproduce in this place this general investigation, which has, moreover, hardly any physiological importance; but, after a few remarks on the most general form of the horopter, we shall take up those special cases which are of most interest.

In the most general case the horopter is a curve of the third degree,—a curve, therefore, which can be cut by a plane in only three points. It may be looked upon as the intersection of two surfaces of the second degree. Surfaces of the second degree intersect in general in a curve of the fourth degree; but in this case the curve of the fourth degree breaks into a curve of the first degree, a straight line which is not part of the horopter, and the curve of the third degree, already mentioned, the *horopter curve*. This curve has two branches, which extend to infinity; they can be conceived as on the surface of a cylinder. Three points through which the curve must go we can at once determine. One of these is the fixation-point (we know that this falls upon corresponding points in the retina), and the two others are the *nodal points* of the eyes. Since these latter points and the parts

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of the curve lying near them are not in reality pictured upon the retina, it follows that the mathematically determined curve has parts which are of no practical significance, but which simply form a part of the solution of the question as mathematically formulated. The curve determined by mathematics Helmholtz, therefore, calls the *horopter curve*, and that portion of it which has an actual significance he designates simply as the *horopter*, or the *point-horopter*. Hering calls it the *total horopter*.

In those cases which we are about to consider more minutely, the curve of the third degree is composed of a straight line and a curve of the second degree; in one case both of these curves lie in one plane, and this entire plane is then the point-horopter.

Besides the point-horopter, we can consider also the *line-horopter* (the *partial horopter*, according to Hering). This is the total collection of those lines in space which are seen singly, without their separate points falling necessarily upon corresponding points of the retina. To the image of a point of one of these lines in one eye may correspond the image in the other eye of some other point of the same line. Lines of this kind whose images fall upon corresponding retinal sections that are parallel to the retinal horizons form, according to Helmholtz, the *horizontal horopter* (the *transversal horopter*, according to Hering). Lines whose images are formed in retinal sections parallel to the middle longitudinal section form the *vertical horopter* of Helmholtz (the *longitudinal horopter* of Hering). In general, the line-horopter is a surface of the second degree.

For greater convenience in the determination of the line-horopter we introduce, with Hering, the idea of longitudinal and transversal planes. If we construct a plane through a visual axis and a middle cross-section, and in this plane form a perpendicular to the visual axis through the nodal point, then the bundles of planes which go through this line are called *transversal planes*. If a plane be drawn through the visual axis and the middle longitudinal section, and in this plane a perpendicular to the visual axis through the nodal point be made, then all planes which go through this perpendicular are called *longitudinal planes*.

We shall now determine the horopter for certain special cases.

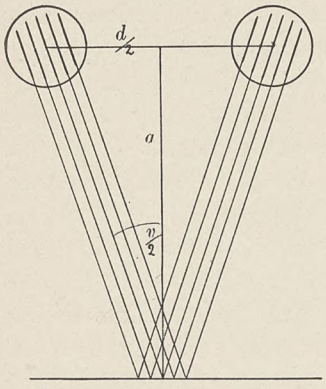
I. *When the Visual Axes are Parallel and Symmetrical with respect to the Median Plane.*—The fixation-point is at infinity. If the middle cross-sections are exactly horizontal, then the transversal planes which cut the retinas in corresponding lines are coincident. In this case, therefore, the entire visual space is the horizontal horopter. If the middle cross-sections, however, form an angle with each other, then the corresponding transversal planes will all intersect in the median plane, and this plane becomes the horizontal horopter. If the middle longitudinal sections are exactly vertical, the corresponding longitudinal planes intersect in the plane at infinity. This is then the vertical horopter. The point-horopter is the intersection of these two line-horopters,—that is, when the middle cross-sections are horizontal. It is also the plane at infinity.

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In general, however, as we know, the middle longitudinal sections form an angle V with each other. In this case the longitudinal planes intersect in a plane that is parallel to the visual plane and at a finite distance from it. This may be perceived from the schematic Fig. 22, which represents a section passing through the retinas and made perpendicular to the visual plane. If we represent the distance between the centres of the eyes by d, and the distance of this line-horopter from the visual plane by a, then we have

$$a = \frac{d}{2 \tan \frac{1}{2} V}.$$

Fig. 22.



Scheme representing a section passing through the retinas and made perpendicular to the visual plane.

If the middle cross-sections are also inclined to each other, the point-horopter is a straight line in the median plane, parallel to the visual plane and at a distance a beneath it. If the middle cross-sections are parallel (which is usually the case), the point-horopter is a plane, and, in fact, the plane beneath the visual plane is situated at the distance a.

According to Helmholtz, the distance a is for him and for many other persons equal to the height of the eyes above the ground. When, therefore, as is usually the case in walking, the visual plane is horizontal, or nearly so, and the eyes are directed to a distant point, the ground is the horopter of points. Images of objects on the ground, therefore, fall upon identical points in the retina. Helmholtz believes that the reason for the convergence of the middle longitudinal sections is to be found in this circumstance.

For the following cases we assume that the middle cross-sections are in the same plane.

II. *The Visual Lines are Symmetrical with respect to the Median Plane.* —The fixation-point is in the median plane and at a finite distance. We assume that the middle cross-sections have remained in the visual plane as the eyes have moved from the parallel position of the visual lines.[1]

The horizontal horopter consists, then, of the visual plane. The reason for this is that the planes of the middle cross-sections lie wholly in the horizontal horopter. This is true for the median plane, for in that plane all the other corresponding transversal planes intersect.

The vertical horopter consists (when the middle longitudinal sections are parallel) of a cylinder perpendicular to the visual plane, whose section by

[1] The motion of the eyes would not then take place in strict accordance with Listing's law. A determination of the horopter in which the departure of the plane of the middle cross-sections from the plane of the visual lines has been taken account of is given by Helmholtz, Physiologische Optik, S. 717.

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that plane is a circle through the fixation-point and the nodal points,—the *horopter circle of Müller*. This is easily understood from Fig. 23, which represents a section through the cylinder in the visual plane. C and C' correspond to the middle longitudinal sections, D and D' to any two corresponding longitudinal sections, A is the fixation-point, K and K' are the nodal points. Then we have $DKC = D'K'C' = \beta$. Hence, also, $KAK' = KBK'$; that is, B is on the circle through K, K', A. The point-horopter is, therefore, this circle and the line perpendicular to it at the fixation-point. When the middle longitudinal sections are convergent, the vertical horopter becomes a cone whose intersection with the visual plane is the same circle of Müller, and whose vertex is the point in which the axes of planes of the longitudinal sections intersect. To find the distance of the vertex from the visual plane, we must consider the section through

FIG. 23.

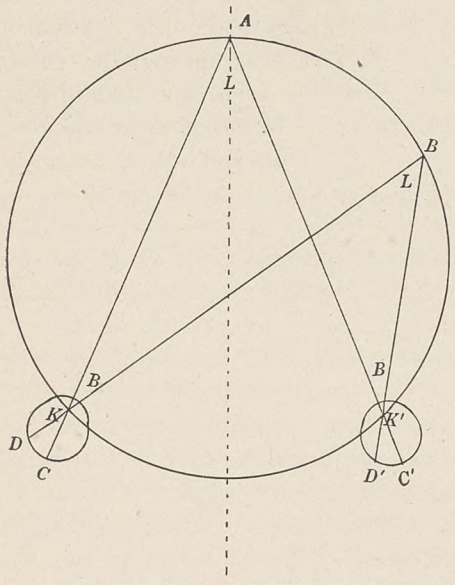


Diagram illustrating the horopter circle of Müller.

FIG. 24*a*.

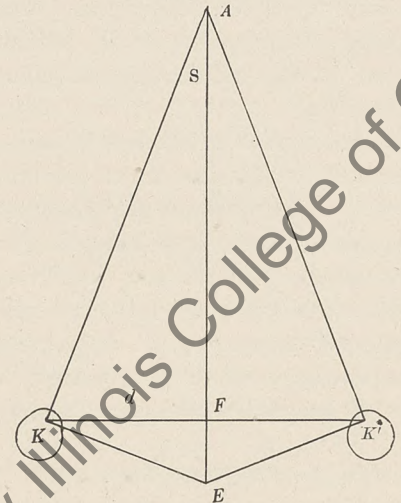


FIG. 24*b*.

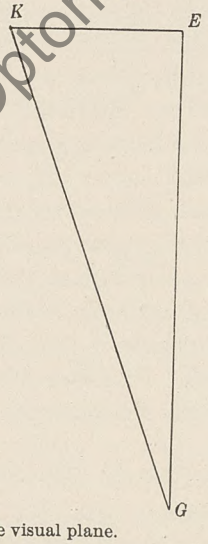


Diagram illustrating section through the visual plane.

the visual plane as represented in Fig. 24*a*. In this figure K and K' are the nodal points, $KAE = \rho$ is half the angle of convergence, $KF = \frac{1}{2}d$ is

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half the distance between the eyes, and KE is perpendicular to KA, the visual line, and therefore parallel to the retina at the visual centre. Then FKE is also equal to ρ, and hence $KE = \frac{d}{2 \cos \rho}$. Construct now through KE a plane perpendicular to the visual line. (Fig. 24*b*.) In the figure KG represents the section of this plane with the plane of the middle longitudinal section, and EG its section with the median plane. KGE is therefore equal to $\frac{1}{2}V$, and hence for the required distance we have

$$EG = \frac{KE}{\tan \frac{1}{2}V} = \frac{d}{2 \tan \frac{1}{2}V \cos \rho}.$$

It follows that the point-horopter is the circle through the nodal points and the fixation-point, and also the straight line through the fixation-point and the vertex of the cone.

III. *The Fixation-Point is in the Horizontal Plane and the Convergence is Unsymmetrical.*—The vertical horopter is a hyperboloid whose section with the visual plane is the Müller circle. The horizontal horopter consists of two planes; one of these is the visual plane, and the other is that plane perpendicular to it which goes through the intersection A of the Müller circle with the median plane, and through one end of the diameter of this circle which goes through the fixation-point. The point-horopter is the Müller circle and a straight line which is inclined to the visual plane and which goes through the just-described point A. (For further details see Helmholtz, "Physiologische Optik," S. 718.)

We have hitherto considered only the horopters of vertical and of horizontal lines. There are other line-horopters, among which we may mention especially the *horopter of meridians*. It consists of those straight lines whose images fall in corresponding meridians,—that is, retinal sections which go through the intersection of the middle longitudinal and cross sections, and which are inclined to them.

What we have just given is the mathematical determination of the horopter based upon the experimental determination of certain identical points. The entire horopter (both for lines and for points) can, of course, be determined experimentally by seeking those lines and points which are seen single while a given point is constantly fixed upon. For this purpose brilliant and strongly illuminated metal wires are made use of, or small metal balls (heads of pins, for instance) are employed. Even candle flames can be used. In this way the empirical horopter is obtained; but much practice in the recognition of double images is a necessary prerequisite.

VI. MEANING OF THE HOROPTER VISION WITH DISPARATE POINTS.

According to what has been said, only those points in space appear single whose images fall upon identical points of the two retinas. Since, for a definite fixation-point, only a single row of points lie in the horopter, only these points ought to be seen single. To these must be added the lines

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which may happen to lie in line-horopters. It would follow, therefore, that, in general, chiefly double images ought to be seen in the visual field, and very few single images. It is plain, however, that this does not in the least agree with experience. So far are double images from forming the chief content of our visual field, that the layman, in general, knows nothing of them, or at most only after his attention has been directed to them by experiment. What is the reason of this? We cannot assume that one of the double images does not usually enter consciousness at all, for then we should not be able to explain the very considerable influence which vision with two eyes has upon the perception of depth. We need especially to consider here that we direct our attention only to those objects which are at the fixation-point or are near it; to those objects, that is, which are in the horopter. If another object engages our attention, we direct the gaze upon it. If we are looking at a somewhat extensive flat surface, it is not the case that we fix upon a single point and allow the attention to wander over the images of the other points; what we do is to allow the visual regard to sweep over the entire surface of the field of view from one point to another. It is, therefore, only the horopter in the vicinity of the fixation-point that is of especial importance. We have to consider the significance of this portion of the horopter; and, further, the double images do not suddenly start up the moment an object is no longer exactly in the horopter. We shall proceed, therefore, to investigate the behavior of points in the vicinity of the horopter.

In the first place, it is easy to convince one's self that the relief of objects which are in the horopter is recognized with the greatest accuracy. For the horopter which is a straight line Helmholtz recommends the following experiment. A pin is slightly bent in the middle, so that it forms an angle of about 175°, and it is then held in the median plane in such a way that both arms of the angle fall as nearly as possible in the horopter line. An eye situated half-way between the two eyes would then see the pin as a straight line. On fixing with both eyes, one recognizes plainly the bending; but if the pin is so moved in the median plane that it no longer lies in the horopter line, the fact that it is bent can no longer be determined.

For the horopter circle one can arrange the experiment in the following manner. Three pins are stuck upright in little wooden supports, and so placed on a table that the heads of the pins are on a level with the eyes. A sheet of paper is held in front of the eyes, so that the lower portions of the pins, together with their supports, are concealed. If the three heads of the pins are in a straight line which is tangent to the horopter circle, one can detect the slightest departure of the middle pin from the straight line. The pins must be rather near to each other, for otherwise an apparent departure from a straight line takes place, from a cause to be mentioned farther on. Helmholtz had the pins placed at the distance of a centimetre from each other and situated about fifty centimetres in front of the eyes. If the middle needle is in the median plane, the power of discrimination

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for the straightness of the line is greatest when the line is at right angles to that plane; but if the right-hand pin is in that plane, then the line must be inclined inward on the left, because it will then more readily coincide with the horopter circle. If the straight line in which the pins lie cuts the circle at an angle, the sensibility to its straightness is considerably diminished.

We have seen that, according to Helmholtz, with most persons (and with himself) the ground is the horopter when the visual regard is directed horizontally forward to a remote point, and that it is sufficiently nearly so when the visual plane is slightly inclined downward, as happens during walking. Helmholtz believes that he has observed that relief in all objects on the ground is particularly well made out when one looks straight forward. It seemed to him distinctly less evident when he looked underneath his arm or between his legs, although he placed himself so high that the eyes were at the usual distance above the ground. That the unusual position of the head did not contribute essentially to the effect was proved by the fact that on looking between the legs, and at the same time inverting the field of view by means of a prism, the original distinctness of relief was again obtained. Helmholtz believes that he has discovered in this circumstance the reason why a convergence in the middle longitudinal sections has been developed. Other physiologists—Hering, for example—have either not confirmed this observation or have explained it differently. It must be remarked that with some observers, Hering among others, the convergence is not sufficient to cause the longitudinal sections to intersect at the ground. The main signification of the horopter lies, therefore, in the fact that in it the perception of relief is most acute.

If a point is moved out of the horopter, so that it is seen with disparate portions of the retina, it continues at first to seem single, although, as in the above-mentioned experiment with the three pins, it is seen not to lie in the horopter circle. Only at a considerable distance from the horopter does it appear plainly in double images. It follows that when the disparateness is not great, double images continue to suffer fusion. On this account, in the determination of identical points we have avoided using lines which overlapped each other, choosing rather such as should come together in a point. Another means for diminishing the fusion of double images is to hold differently colored glasses before the two eyes, or to have the two fields of the haploscope of different colors. For the same reason Fig. 21 is drawn white on black on the right-hand side and black on white on the left-hand side.

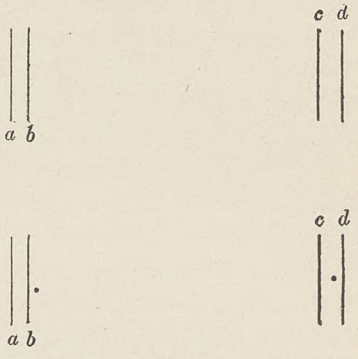
The amount of disparateness at which images cease to fuse is different for different observers. It also depends much upon practice: the experienced observer can separate double images when they are very near together. The volition of the observer and the direction of his attention are also of great effect in the matter of fusion. If one makes an effort to hold in mind the idea of position in space, double images are readily fused; but if one endeavors to compare the two monocular fields of view, the images

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are more easily seen separate. Another means of separation is to have slight inequalities in the two figures to be united,—on one a little mark on the right of a line, in the other on the left. In this way the belief is disturbed that the two images are derived from a single object.

If, in the haploscopic drawing, Fig. 25 (above), in which the lines *a* and *b* are 3.2 millimetres apart and *c* and *d* 4.6 millimetres, *a* and *c* are fixed upon with the right and the left eye respectively, *b* and *d* will unite also, the line *bd* appearing either behind or in front of *ac*. If, however, one introduces a point to the right of *b* and to the left of *d* (as in Fig. 25, below), and fixes as before, the point is seen single, and then one easily succeeds in separating the lines *b* and *d*.

Fig. 25.



Haploscopic drawing illustrating disparateness and fusion.

It is worthy of remark that vertical lines fuse much more readily than horizontal ones. Helmholtz takes the reason for this to be that in looking at actual objects the differences between vertical distances upon the two retinas is generally much less than between horizontal distances.[1]

Volkmann has made experiments upon himself and others by means of a haploscopic arrangement corresponding to Fig. 25 (above), but with one thread, *d*, movable, so that it could be adjusted at different distances from *c*, in order to see whether, with great disparateness, fusion will still occur. The absolute findings are not, of course, of much consequence, on account of individual differences, but they give an indication of the course of the fusion. We give the following table:

Observer.	Distance apart, in millimetres.			Direction of Lines.
	ab	*cd.*	*ab–cd.*	
V.	5.3	3.46	+ 1.84	Vertical.
		7.57	— 2.27	
V.		4.88	+ 0.42	Horizontal.
		6.05	— 0.75	
T.		2.13	+ 3.17	Vertical.
		10.00	— 4.70	
T.		4.66	+ 0.64	Horizontal.
		5.91	— 0.61	
K.		3.21	+ 2.09	Vertical.
		8.48	— 3.18	
K.		4.92	+ 0.38	Horizontal.
		5.86	— 0.56	

[1] Is it not rather because in real life, on account of the fact that we have not an upper and a lower eye as well as a right and a left eye, actual horizontal lines are never seen in double images (provided the middle cross-sections are in the same plane)?

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The arrangement was equivalent to the observation of lines one hundred and fifty millimetres in front of the person looking. The individual differences are evident, and also the difference between horizontal and vertical lines.

The latter difference one perceives also in looking haploscopically at two circles of slightly different diameters. Here the vertical portions unite when the horizontal portions are distinctly seen as double.

Volkmann has also made experiments concerning the greatest differences in direction which can be overlooked with different inclinations of the fixed line to the vertical. In this case it appears that nearly vertical lines unite much more readily than those which are nearly horizontal.

If disparate points and lines can be seen singly, it has seemed to some persons to be a logical consequence that points whose images fall upon identical portions of the retina can be seen double. We have seen that in Fig. 25 the right-hand lines unite when the left-hand lines are fixed upon. Those portions of the diagram which correspond to the two points of the lower figure now fall upon identical points in the two retinas. They, however, lie the one to the right and the other to the left of the single image *cd*. We cannot introduce these points into the drawing, because the fusion of the two lines would be interfered with. Wheatstone, who first gave expression to the view that we can see double with identical points, endeavored to prove it by the diagrams drawn in Fig. 26. The heavy line on the left corresponds to the fine line on the right, while the heavy line on the right is inclined to that at an angle of 10°. On uniting them haploscopically the two heavy lines fuse. Helmholtz has remarked that for eyes accustomed to the separation of double images the inclination is too great; he has changed the experiment somewhat, and he has also added the experiment represented in Fig. 27. In such a figure the fields *A* and *B* are to be colored red, *C* and *D* green, and the points *f* and *g* are to be fixed upon. The two small crosses *i* and *h*, which indicate two points which are impinged upon identical portions of the retinas, must not be drawn. Upon haploscopic fusion the borders of the diagrams unite, and also the lines *ab* and *cd*, and one gets the single impression of a surface which is inclined to the vertical direction and which is half green and half red. The points indicated by the crosses, therefore, are, in accordance with Wheatstone's view, red for one eye and green for the other. According to Helmholtz, these experiments teach us that "as long as one is absorbed in the contemplation of objects or solid bodies, even when the fixation-point is kept constant, corresponding impressions are utilized to fill out different portions of the total corporeal image." This view, however, has found many opponents as well as many defenders. Among the former

FIG. 26.



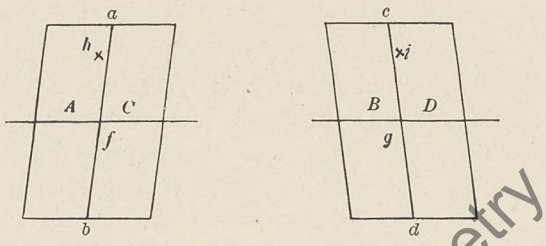
Wheatstone's diagram to prove double vision with identical points.

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is Hering, who interprets the experiment concerning the fusion of the lines *ab* and *cd* to the effect that the sensations corresponding to places indicated by the crosses do not enter consciousness at all, but that the sensation of color on either side of the bounding line always agrees with the position of that line.

In the different experiments which we have described concerning single vision, a given point has been required to be constantly fixed upon. We cannot, however, be absolutely certain that the visual regard has not wandered from time to time to another portion of the field of view, and that this wandering, which plays such an important part in vision in common life, has not been of some influence in the perception of depth. Brücke has, in fact, proposed the hypothesis that seeing single with disparate points is only apparent, and that the conception of space is acquired through the constant wandering of the visual regard, by means of which one point after another throws its image upon identical points and is in consequence seen single. This view is contradicted by experiments in which the picture is

FIG. 27.



Helmholtz's diagram to prove double vision with identical points.

offered to the eye for so short a time that there is no possibility of a change of the point of convergence. In the first place, Dove showed that in instantaneous illumination by the electric spark, perfect perception of depth is obtained with the stereoscope. In order to keep the fixation-point constant when the illumination is not obtained by the electric spark, Aubert pierced fine needle-holes in corresponding points of two stereographs, and illuminated them from behind. In this experiment also there was a perfect effect of depth without the needle-hole appearing double. Aubert, indeed, has found that, with instantaneous illumination, the spatial conception prevails in cases where, with a longer illumination, one can choose between bringing to consciousness double images with no depth concept, or a single picture with extension in depth. For instance, if a vertical line is presented to one eye, and to the other there is given a line inclined at an angle of 10°, one can see at pleasure either two lines crossing each other or a single line in a definite position in space.

Hering has devised experiments which have had the same result. He looked through a short tube at a needle which was placed at a convenient distance beyond the tube, while his assistant dropped little balls of different

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sizes at varying distances in front of and behind the thread. The observer could always tell with certainty whether the course of the ball was behind or in front of the needle. Rogers has succeeded in producing after-images of stereoscopic drawings in corresponding eyes, and in uniting them afterwards into the picture of an object in space.

If points in space are outside the region within which fusion of double images occurs (*stereoidentical points* in the nomenclature of Aubert), double images are plainly visible, and such images might have been supposed to be of less consequence in the perception of depth; but in Hering's experiments with the falling balls it was found that the distance of a ball could be given no less correctly when it appeared plainly in double images.

VII. LOCALIZATION.

It was said in the beginning that we project outward into space excitations by light which reach us as sensations, and that we refer every such excitation to a more or less definite point in the visual space. We shall proceed to determine the laws for this projection, and to test the accuracy and the correctness of such localization.

Very distant objects, even when looked at with two eyes, we localize, as we have seen, when other means of knowledge are wanting, in one and the same distant surface. In this case it is, therefore, in general a matter of indifference whether we see with one or with two eyes. So also when we look at nearer objects which are nearly in the vertical horopter; this case occurs when the object is a plane of small extent perpendicular to the plane of regard (the convergence being symmetrical). In all these cases, and in all vision with one eye, only the form and the size of objects are taken account of. In general, we localize within a given plane both correctly and accurately; we compare different objects by means of movements of the eyes; equal lines, for instance, we picture one after another upon the same portion of the retina. We need only consider here those departures from correct localization which appear when the eyes are at rest. One error of this kind we have already noticed; it follows from the convergence of the middle longitudinal sections. In consequence of this, a right angle with one horizontal and one vertical side is not seen as rectangular. It was pointed out that the right side of Fig. 21 represents a rectangular grating for the right eye, the left side for the left eye.

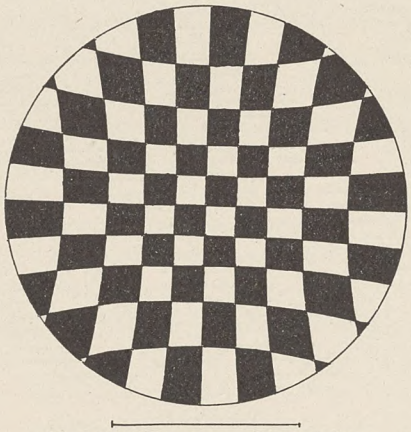
Other illusions are the following. Select three stars in the sky, at a considerable distance apart, which seem to lie in a straight line when the eye wanders along this line; if they are looked at with the periphery of the retina, they will seem to be in a curved line, concave towards the fixation-point. If the drawing given in Fig. 28 be enlarged n times (five or ten times, for instance), and held at a distance from the eye equal to n times the line underneath it, the eye being just opposite the middle of the drawing, and this point being fixed upon, then, according to Helmholtz, the appearance of a rectangular, chess-board-like figure is obtained. (For

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the explanation, and for other illusions connected with this, see Helmholtz, "Physiologische Optik" (1st ed.), S. 582, ff.) The curves in the figure are hyperbolas.

A given distance seems to be longer if it is cut up into subdivisions. Thus *AB*, in Fig. 29, looks longer than *BC*, although it is in reality

FIG. 28.



Chess-board-like figure of Helmholtz.

of exactly the same length. Acute angles appear too thick, obtuse angles too slender. In Fig. 30, for example, *ef* appears to be the continuation of *ab* instead of *cd*, although *cd* is really in the same line with it. In this way is explained the illusion of Zöllner, which is illustrated in Fig. 31. The long lines, which are inclined 45° to the horizontal direction, are in reality parallel, but they seem to be alternately convergent and divergent.

FIG. 29.

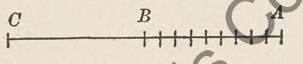


Figure showing subdivided line.

FIG. 30.

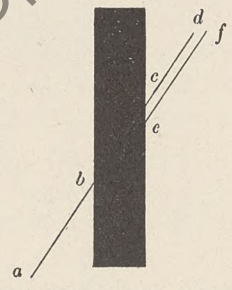


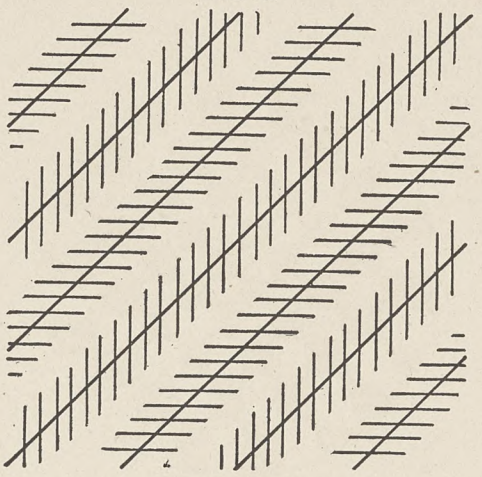
Figure showing apparent increase of acute angle.

If we assume that the apparent increase of the acute angles formed by the short cross-lines with the long ones proceeds in such a way that both sides of an angle are turned from their true direction, the illusion may be considered to be dependent upon the size of the angles. Opinion, however, is much divided as to the proper explanation to be given of this and other similar illusions.

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As regards the direction in which we localize, it is clear that in vision with one eye we refer objects to some point in the line of sight: that is a consequence of the laws regarding the formation of the image in the eye.

FIG. 31.



Zöllner's lines.

It is quite otherwise, however, as was first shown by Hering and Towne, when we observe, as is usual, with both eyes. If in Fig. 32 we fix upon an object, *a*, the point of a needle, say, at the distance of distinct vision, we see

FIG. 32.

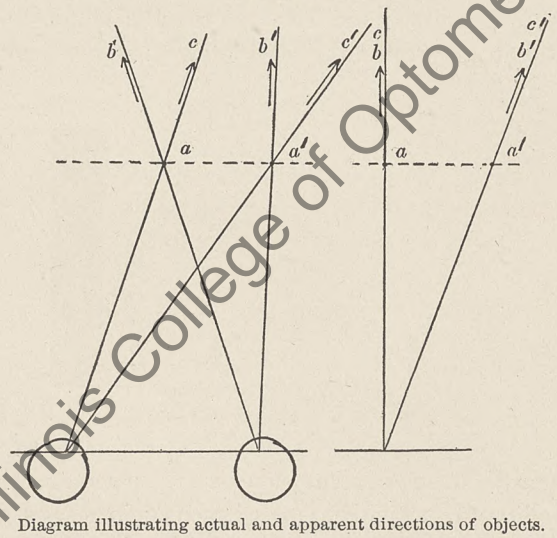


Diagram illustrating actual and apparent directions of objects.

other objects at the same time; for instance, an object *b* somewhere behind *a* in the line of sight of the right eye, and an object *c*, also behind *a*, but in the line of sight of the left eye. If, while fixing upon *a*, we direct the at-

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tention to b and c, we shall notice that the images a, b, and c all reach the eye in the same direction. If the object a is in the median plane, this direction of projection is also in the median plane. Introduce now another point, a', which is in the horopter, and whose images, therefore, fall upon identical points. On the sight-line of the right eye belonging to a' place another object, b', and on that of the left eye another object, c'. The projection-lines of a', b', and c' coincide the same as before. These lines are called the *lines of visual direction*, and among them that which contains the fixation-point is called the *principal line of visual direction*. The obscurely seen objects b, c, b', c', appear, of course, in double images, but such images are frequently so far apart that we are conscious only of the one here taken account of. Objects which lie really on very different lines, and even on different sides of the head, are, therefore, localized on one line. There is a certain pair of sight-lines to which a single direction-line corresponds in such a manner that all objects on either of these sight-lines appear to be on one and the same direction-line. There arises, therefore, a sheaf of direction-lines, all of which proceed outward from a single centre. The position of this centre is, for normal individuals who are in the habit of using both eyes equally, situated half-way between the two eyes, at the base of the nose. If we suppose an imaginary eye to be situated at this place, to which the images of the two actual eyes are transferred in the proper manner, then the sight-lines of this single eye will correspond to the lines of visual direction in binocular vision. This imaginary eye has been called the *Cyclopean eye*. For persons who are in the habit of using only one eye—for those who work much with the microscope, for instance—it may be customary to refer the directions of objects to that eye only; but, as before, objects which are pictured upon the same points of the retina seem to lie in the same direction. The illustration of this relation, which is given in Fig. 32, is due to Hering. The drawing on the left represents the directions of objects as they actually are, and that on the right their directions as they appear to be.

From what has just been said, it follows that whatever is pictured upon the middle cross-section of the retina seems to be situated in a plane which divides the visual space into an upper and a lower half. Hering calls this plane the *middle cross-plane of the visual space*. So everything which is pictured upon the middle longitudinal section is localized in a plane which divides the visual space into a right and a left half,—the *middle longitudinal plane*.

We shall now investigate the effect upon localization of images which fall on disparate portions of the retina, when the images are so near together as to be nearly or completely fused. We have seen that we estimate with great accuracy the relative position of objects which are nearly in the horopter. If we look at a row of vertical threads hung in a plane at right angles to the median plane, and consequently nearly in the vertical horopter, and if we move one of the threads a little out of the plane, we can easily detect the change. We can also determine whether the thread which has

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been moved is in front of the other threads or behind them. In both cases there is disparateness of images in the transverse direction; but when the thread is in front of the plane, the left-hand image has been moved to the right and the right-hand image to the left (*heteronymous images*); and when the thread is behind the flame, the left-hand image has been moved to the left and the right-hand image to the right (*homonymous images*). The eye, it is therefore evident, is able to distinguish between heteronymous and homonymous images, and to make use of this distinction in localization. This fact disproves the view of Johannes Müller, that corresponding portions of the retina play a like *rôle* in localization. In Fig. 33, let *a* be the

FIG. 33.

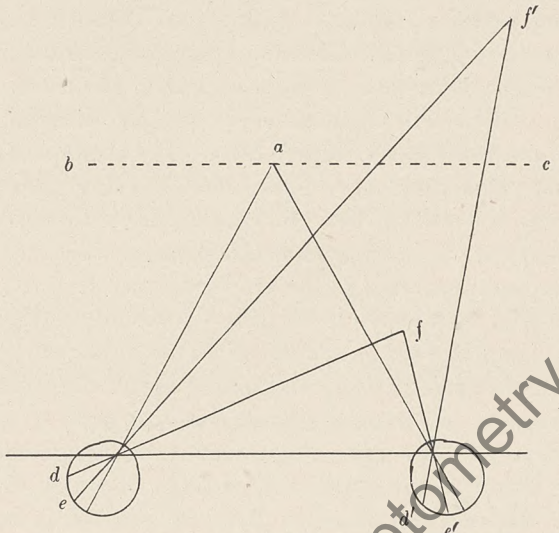


Diagram illustrating heteronymous and homonymous double images.

fixation-point and let *bc* be the tangent to the point-horopter. Let *d* and *d′* be identical retinal points, and also *e* and *e′*. Sight-lines from *d* and *e′* will intersect in a point within the horopter, as *f*, and lines from *d′* and *e* will intersect in a point without the horopter, as *f′*. In the one case the double images are heteronymous, in the other they are homonymous; and the fact that we can readily tell whether the thread has been moved forward or backward shows that we can distinguish between these two conditions.[1]

[1] The subject of localization has been put upon quite a different footing by means of an experiment of Schön's. (Archiv für Ophthalmologie, Bd. xxi. See also Nature, February 13, 1896.) He finds that the circumstance which is really of moment in distinguishing between an object at *O* and one at *I* (outside and inside the horopter circle) in Fig. 33*a* is not that in one case the right eye sees the right image and the left eye the left image, while in the other case the images are crossed, as it is impossible that the eye can tell whether certain imaginary lines in space are crossed or not. The determining difference is due to the fact that the nasal half of the retina sees objects much brighter than the temporal half, and that in the one case the bright image is farther from the fovea than the faint image, and in the other case it is nearer to it. An object at *O* is seen by means of

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The thread, which in the above experiment was moved out of the plane of the others, gave disparate images in the transverse direction only.

If we rotate the threads by 90°, keeping them still in the same plane, so that they are horizontal and parallel to the plane of visual regard, and then move one thread a little out of its plane, its departure from its original position cannot be detected. In this case the disparateness is longitudinal, and it follows that that is of very little influence (according to Helmholtz), or of none at all (according to Hering).[1]

In these and in the following experiments it is necessary to have a plain background against which the objects to be looked at are sharply defined.

If, with the primary position of the head (upright and directed straight forward) and with a horizontal position of the plane of regard, one fixes his vision upon a thread suspended in the median plane, and if the thread is then rotated in the median plane about the point of fixation, the upper and the lower halves of the thread are seen in double images, one pair being heteronymous and the other homonymous. In each pair, however,

---

the double images n' and t, an object at I by means of the double images t' and n. In both cases the images fall upon points of the retina which correspond to the points A and B of the horopter circle; but in the one case (outside) B represents the position of the bright image and A the position of its shadowy attendant, and in the other A is the position of the bright (nasal) image and B that of the (temporal) shadowy attendant. That this difference in brightness is a sufficient criterion for locating outside or inside the horopter circle (there may be others, as size of image, color, etc.) is absolutely proved by this ingenious device of Schön. Instead of placing actual objects at the points O and I, he has objects, which must be identical in appearance, somewhere in the sight-lines through O and I, but farther away, as at the points N, N', T, T'. The objects N' and T form images at n' and t; the objects N and T' form images at n and t'. If now all the other images of these objects are carefully cut off by little screens, then the most probable interpretation of what is seen is that there is in the one case a real object at O, and in the other a real object at I, the nasal and temporal distribution of images being such as real objects at these points would effect. By changing the actual relative illumination of the objects N' and T, however (by throwing light on T by means of a mirror, or by putting a gray glass in front of N'), Schön changes the relative brightness of the images n' and t; that is, he causes the image which is near the fovea (t) to be brighter than that which is farther away (n'). This is the condition for believing an object to be at I, and in fact he has succeeded in this way, with most observers, in changing the apparent position of the illusory object from O to I, or back again, at pleasure. The rule for localization should, therefore, be stated thus: we localize outside the horopter circle when the principal image (the image formed by the near eye) has a shadowy attendant on the inside (that is, nearer to the fixation-point); and we localize inside the horopter circle when the principal image has a shadowy attendant on the outside (that is, farther from the fixation-point). In both cases, therefore, there may be said to be a sort of heteronymy.—Trans.

FIG. 33a.

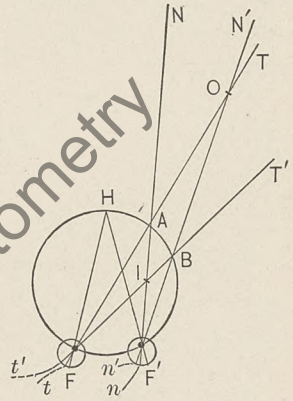


Diagram illustrating Schön's experiment.

[1] In other words, we are provided with two eyes in a right-and-left direction, but not in an up-and-down one.—Trans.

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one image is moved as far to the right as the other is moved to the left. In such a case as this the double images are said to be symmetrical. From the fact that the thread is constantly referred to the median plane, we conclude that points whose disparate images fall symmetrically on either side of the middle longitudinal section are referred to the median plane. If, under the same conditions, one looks at beads which are in a horizontal plane at the level of the eyes, partly in front of and partly behind the horopter, and if one bends the head forward and backward, keeping the fixation-point constant, the middle cross-sections become inclined to each other, and the images of the beads, in consequence, become symmetrically disparate in a longitudinal direction. In this case, also, they continue to be referred to the plane in which they actually are,—the plane of the middle cross-section.

A vertical thread, looked at with symmetrical convergence and with the plane of regard horizontal (the head being in the primary position), appears, according to Helmholtz, to be vertical, in spite of the fact that, on account of the convergence of the middle longitudinal sections, the thread can be plainly seen (if it is sufficiently long) to furnish double images. According to Hering, the thread appears to be vertical when it coincides with the straight line of the point-horopter.

If, while looking at a vertical thread, one inclines the head backward, the plane of regard being still horizontal, the lower end of the thread seems to be nearer to the observer: this proceeds from the fact that with this movement of the eyes the middle longitudinal sections converge more above. According to Hering, the apparent vertical position of the thread is obtained (upon moving its lower end backward) when its images fall upon the middle longitudinal sections. Helmholtz says that it is obtained when they fall upon the same (disparate) sections upon which the images of a vertical line fall when the head is in the usual position.

A row of threads in a vertical plane perpendicular to the median plane seems to lie in a plane that is convex towards the observer (provided the outer threads are seen under a sufficiently great angle).[1] In order that they may apparently lie in a plane, they must actually be in a surface slightly concave towards the observer. Hering holds that this surface, whose intersection with the visual plane is of less curvature than the Müller circle, is the real vertical horopter, the arrangement of the identical points not corresponding exactly, in his view, with the representation which we have given of them. Helmholtz asserts that the apparent curvature is to be explained by the fact that we are in the habit of underestimating distances.[2]

[1] In the experiments hitherto described with threads, it was assumed that they were so near together that the departure of the horopter circle from a straight line might be neglected; and so also in Helmholtz's experiments with the three needles.

[2] From the above it appears that disparateness in a longitudinal direction alone has very little effect in changing our localization of objects. It follows that we localize points whose images are either identical or differ longitudinally only in a surface which we shall call the fundamental surface (Kernfläche of Hering). According to Hering, this surface seems to us to be a plane: according to Helmholtz, it appears to be slightly concave towards the observer.

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If we have three threads, *a*, *b*, and *c*, in a vertical plane, *b* being in the median plane and *a* and *c* at equal distances to the left and to the right, there is the portion of the retina which corresponds to the distance *ab*. This is less in the right eye than in the left eye, and that which corresponds to *cd* is greater in the right eye than in the left eye. The difference in these retinal distances is (for a given distance of the threads in front of the eyes) a mark by means of which we estimate the surface to be concave, convex, or plane. If now we refer the threads to a distance that is less than their actual distance from the observer (every other means of estimating distance, except the feeling of convergence, being absent), we shall see the surface as convex. If, however, there are beads on the threads, the illusion in regard to the curvature of the surface of the threads will not take place.

If one looks at lines, or wires, which go through a point, and which lie in a plane that is perpendicular to the median plane and to the visual plane, the visual regard being directed upward and the intersection of the lines being the fixation-point, the upper lines of a star will seem to be in a concave surface of a cone, as v. Recklinghausen has shown, while the lower lines appear convex. This also is explained by the fact that, on account of the movement of the eyes, the middle cross-section is no longer in the visual plane. The surface in which the lines must lie, if they are to seem to be in a plane that is perpendicular to the median plane and to the visual plane, is, according to theory and to v. Recklinghausen's measurements, a cone of the second degree. For eyes with parallel longitudinal sections, the surface is the horopter of meridians for the given position of the eyes: v. Recklinghausen designates it as the normal surface.

That the degree of convergence has an effect upon the distance at which we localize an object is beyond a doubt. If stereoscopic pictures are introduced into a mirror haploscope and a given point is fixed upon (the axes of the eyes being convergent), and if the mirrors with the pictures are then so rotated that the convergence is diminished, the objects looked at will seem to move farther away. Moreover, since the visual angle remains the same, they will appear to become larger. Wundt has made experiments to determine with what degree of exactness changes of distance can be estimated by change of convergence alone,—this being accomplished by means of a thread suspended in the median plane in front of a white background and moved forward and backward by a degree of motion that can be measured. During these experiments Wundt found that when the thread was at a distance of one hundred and sixty centimetres the change of distance that could be just detected (whether the thread was placed nearer or farther away) was three centimetres, whilst for a distance of fifty centimetres it was one centimetre. The estimation was, therefore, very exact.

Wundt has also made experiments on the exactness of our estimation of the absolute distance of a thread, and has found it to be very slight; the distance was always underestimated. His results (in centimetres) were these:

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Actual Distance.	Estimated Distance.
180	120
120	58
80	47
40	25

He says that very distant objects are judged to be too near when other means of correcting our judgment are wanting,—when, for example, we do not know their actual size. This is a matter of daily experience, as in the case of distant lights, the moon, the sun, and the stars.

Finally, we have to consider localization in those unusual cases in which objects which are actually double seem to us to be single. This happens, of course, when we use the stereoscope and the haploscope. With the stereoscope, however, a number of different considerations derived from experience have a determining influence. We are more interested in those cases in which such extraneous considerations are wanting, and in which also comparison can take place with actual objects in space.

If we stand in front of a distinct wall-paper pattern, we can, by the use of strong convergence, cause one figure of the pattern to overlap the adjoining one. The image which we see then seems to be swimming in the air in front of the wall. If one looks at a distant point, and if a needle is held in each line of sight, two images of two needles can be brought into fusion with each other. A thicker needle will seem to be seen at a greater distance. In this case, therefore, we localize in accordance with convergence. If two like coins are placed on a table at a distance apart that is equal to the distance between the eyes, and if their images are made to coincide, the lines of sight being parallel, the coins are not localized at the distance that they should be in accordance with the convergence. This is so on account of the influence of the near table and other objects on it. If, however, the same coins are united with the lines of sight crossed, a small coin will be seen, as in the case of the wall-paper pattern, floating in the air.

Upon summing up the facts which we have described in this section, we come to the conclusion that for those portions of the field of view to which the attention is customarily directed—the fixation-point and its immediate vicinity—the accuracy as well as the correctness with which we localize objects is very great; the exceptions are, in comparison with the extent of the phenomena that are presented to us, unimportant.

VIII. RIVALRY OF VISUAL FIELDS AND OF CONTOURS.

We have now to discuss certain phenomena which escape our observation in the ordinary use of the eyes for practical purposes, and which are discovered only upon making experiments with the stereoscope and the haploscope, but which are nevertheless of much importance for the better comprehension of the processes of binocular vision.

In the experiments with the haploscope for the determination of the identical points of the retinas we have repeatedly used fields of such a character that on one side was represented a black line on a white surface,

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while on the other side there was no such line. At the same time certain other lines appeared alike on both sides. In these experiments we were able to state that in the first case the black lines presented themselves in the binocular field exactly as in the second; that is to say, they were not gray, as one might have expected on account of the fact that the corresponding portion of the other retina was at the same moment receiving the sensation of white. If in one haploscopic field we have two large letters, *A* and *B*, and in the other two similar letters, *B* and *C*, and if we unite the two fields in such a way that *B* falls upon identical parts of the two retinas and is seen single, with *A* on one side of it and *C* on the other, then all three letters look alike black on a white ground. If, when reading a book, we hold a sheet of white paper before the left eye, the white ground of the printed page seems about equally bright whether the left eye is kept open or shut, though in one case the left field of vision is white and in the other it is nearly black. The white paper in front of the left eye produces some effect only if it is brilliantly illuminated, as by the sun.

FIG. 34.

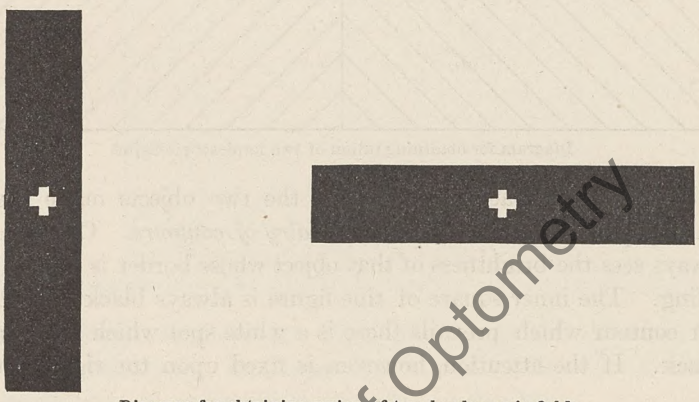


Diagram for obtaining union of two haploscopic fields.

We shall now consider two haploscopic fields containing diagrams which, upon being united, partially coincide with each other. To make the experiment as simple as possible, we choose fields such as those in Figs. 34 and 35. In Fig. 34 we have on the left a long, rectangular, black field perpendicular to the visual plane, and on the right a similar black field situated at right angles to the first. In the middle of each field is a white cross. The fixation-point is kept steady by causing these white crosses to coincide with each other. In the binocular field we have now an appearance which cannot be very well represented in a drawing, but which, in succession, appears something like what is given in Fig. 36, *a*, *b*, and *c*. (The fixation-crosses are here left out.) At those parts where the contours of one black band overlap those of the other there is a continually wavering appearance, as if there was a constant rivalry between the two impressions which it is possible for the object to convey. This phenomenon has,

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in fact, been called the *rivalry of the retinas*. The impression obtained is not for a moment that of an evenly black or evenly gray cross. On the parts where the black bands overlap each other, one sees now the contour of one band, now that of the other, and again both at once, as in *b*,—these being so provided that the attention is allowed to wander, and also that (as in our diagram) there is no unlikeness in the intensity of the two fields.

FIG. 35.

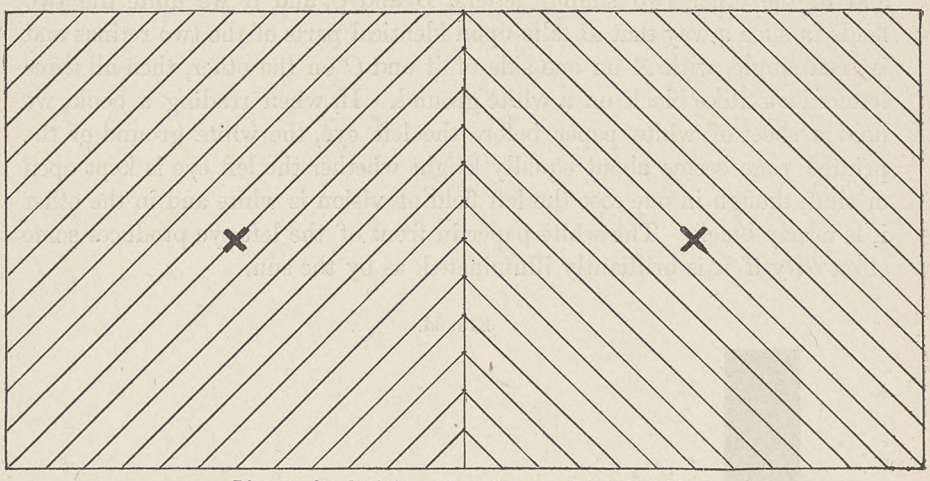


Diagram for obtaining union of two haploscopic fields.

This circumstance—that the borders of the two objects make themselves particularly prominent—is called the *rivalry of contours*. Close to an edge one always sees the brightness of that object whose border is for the moment prevailing. The inner square of this figure is always black. Just outside of each contour which prevails there is a white spot which goes gradually into black. If the attention, however, is fixed upon the right-hand band,

FIG. 36.



a *b* *c*

Diagram illustrating the effect of the union of the two haploscopic fields in Fig. 34.

a is the impression which prevails; if it is directed upon the left-hand band, *c* represents what is seen.

In the second case (Fig. 35) each field contains a series of black lines at equal distances from each other, and inclined at an angle of 45° with the visual plane, running from right to left on one side and from left to right on the other. Upon uniting these haploscopically, we do not see a field of perfect squares, as in Fig. 37, but simply notice a wavering image whose separate parts correspond now to the right-hand, now to the

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left-hand figure. This is the appearance when no particular direction is given to the attention; but if the attention is fixed upon either half of the diagram,—if, *e.g.*, we endeavor to count the lines of one half, or if we let the visual regard wander along the lines,—then the half that is regarded distinctly prevails for some moments over the other.

Helmholtz explains the rivalry of the visual fields as being due to the wandering of the attention, and finds in the overpowering influence of contours the effect of habit, which leads us to examine especially the contours of any object that is presented to us in order that we may recognize as quickly as possible what the object is. The phenomenon is a proof that

FIG. 37.

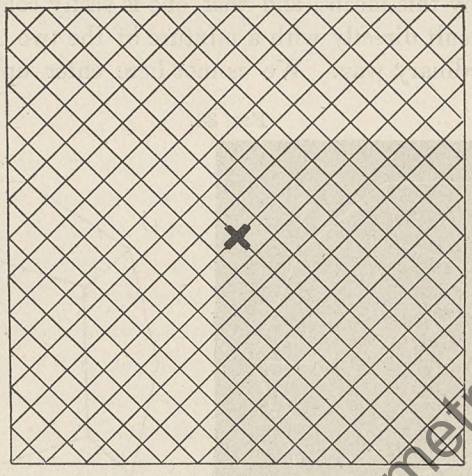


Diagram illustrating the effect of the union of the two haploscopic fields in Fig. 35.

the contents of each field of view reach consciousness distinct and separate from those of the other. It also teaches us that such fusion as takes place is not conditioned by the organic structure of the brain. The bearing of the phenomenon upon our powers of perception consists in its showing that when a fusion of the sensations of the two fields does not occur (in accordance with the laws above explained) in the interests of the perception of a third dimension, each field of vision preserves its independence.

IX. BINOCULAR COLOR-MIXTURE; LUSTRE.

The rivalry which we have just described occurs also when the two fields are differently colored,—when, for instance, one looks at an object with a piece of red glass held before one eye and a piece of blue glass held before the other. The glasses must be so chosen that the object is of about the same brightness when looked at through the two glasses separately. At the first moment the field of view seems to be irregularly spotted in red and blue, the two colors appearing alternately in rivalry over the whole field. After some time a condition of greater repose sets in, and a more or less single impression is obtained (which is considered by many

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physiologists to be a mixture of the two colors). Instead of the colored glasses, two Nicol prisms may be held before the eyes, their planes of polarization being placed at right angles to each other; or we may look through thin plates of gypsum or of mica at a surface which reflects light at the angle of polarization. By this means the two eyes see colors which are exactly complementary to each other. On rotating the Nicol prisms, the planes of polarization remaining perpendicular to each other, different pairs of colors are obtained. One can also unite haploscopically two fields which are differently colored by pigments.

Many physiologists affirm that in these cases a mixing of the colors is obtained, while others are just as positive that the correct color of fusion is never obtained by this means, and that one is easily convinced of this by comparing the result directly with a mixture of the two colors brought together in the ordinary way. We cannot here enter upon the numerous

FIG. 38.

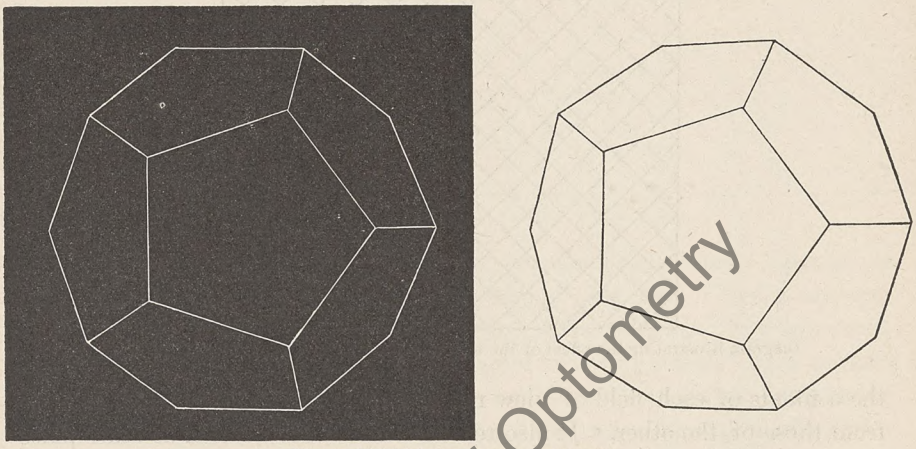


Figure for obtaining stereoscopic lustre.

experiments which have been devised and described in order to settle this point. Individual differences evidently play an important *rôle* in the phenomenon. Thus much, however, appears to have been plainly made out: the phenomenon of a fusion of colors occurs only under definite and carefully chosen conditions; it is very easily disturbed by the slightest differences in the two fields of view, which are sure to bring out rivalry; exactly the same effect as is obtained by monocular mixture of the two colors (with the color-wheel, for instance) is seldom or never produced, but rather a mixture which lies vaguely somewhere between the two.

It is also of importance that the colors to be mixed should be of somewhat the same brightness, for otherwise a peculiar effect is produced. This is that of stereoscopic lustre, first discovered by Dove. A glance at Fig. 38 with an ordinary stereoscope will show very well what is meant, and the condition assumed.

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NORMAL COLOR-PERCEPTION.[1]

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THE rainbow may be regarded as one of the best examples in nature to show us not only the beauty of the pure colors but also the subjective aspect of them. Though the times have long gone by when Iris was thought to bring down along this path her message from the gods, nevertheless many people still regard the rainbow as an objective thing, and they wonder when scientists tell them that every person must of necessity see his own rainbow, differing from that of his neighbor not only in apparent size, according to the size of the observer, but also in its apparent position in the sky. And this may serve as a good illustration of the great difference between the old crude and the modern scientific view. Formerly all the qualities of the surrounding objects were regarded as something inherent in them, something that existed there independently of ourselves, whilst now we have learned to regard each quality in nature as a product of two factors, the *external object* and the *perceiving subject*. But this analysis is not always easy, and it seems especially difficult to separate the subjective and the objective factor with regard to colors; so difficult that artistic minds like Goethe's find it impossible to do so, and turn away with disgust from an analysis of our color-perceptions. Still, there is no escape from it, and it will be the object of this paper to review some of the most important facts with regard to the subjective and the objective aspect of colors. Of course, in the space allotted to this subject it will be impossible to go fully into details or to enter upon an exhaustive discussion of the different theories, especially in face of the fact that there are a good many questions still unsettled.

First, then, *What is color objectively?* To answer this we must know

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[1] The reader is referred to the papers of Professors Piersol, Cattell, and Mays in connection with this subject.

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what light is objectively. Light is regarded by modern physicists as a form of movement in a hypothetical medium, the ether. This is the undulation theory of light, which explains very completely all the phenomena so far observed. According to this theory, all the particles of ether along a ray of light are moving in straight or curved lines near their original points of equilibrium, like a pendulum, this movement occurring at right angles to the direction of the ray. As the movement of each succeeding particle occurs slightly later than that of the foregoing, it is clear that a line touching all the particles in their momentary positions, beginning at the first particle when this is just coming back to its original position and extending to that particle which just starts to move, must have a form like this :  . The distance between the end-points of this wave-line is called the wave-length, and is the smaller the sooner each particle completes its oscillation; whilst the velocity with which this oscillatory movement propagates itself in the air is the same for all wave-lengths, amounting to about one hundred and ninety-two thousand miles per second. If in a ray every particle of ether moves always through the same path with the same velocity, we call the light thus resulting monochromatic or homogeneous light: each particle takes then the same amount of time for its excursion. As soon, however, as, in another ray, the time of oscillation of each particle decreases, and as, therefore, the wave-length gets smaller, then again we get simple light, but of a different quality for our eye, or, as we express it, of a different color. Physically, therefore, color finds its equivalent in the number of oscillations per second, or the wave-length, and it has been found by experiment that light of the lowest number of oscillations of the ether particles and the greatest wave-length gives us red, while light of the smallest wave-length gives us violet. We speak here of greatest and smallest wave-lengths, but it must be understood that this refers only to those ethereal waves that are perceived by us as *light*. Indeed, the ether particles are capable of all kinds of oscillation, and in the ether waves of all lengths may be excited and propagated. The long waves seem to belong to the domain of electricity and magnetism, according to the recent brilliant researches of Hertz. They do not seem to affect us directly; at least we have no special organ for their perception. They have been investigated by purely electrical methods, and those electro-magnetic waves that have been measured have been found to range from a few inches to many yards. The shorter waves affect our nerves in the skin and produce heat as soon as they are 2760[1] $\mu\mu$[2] long,—*i.e.*, when there are about one hundred billions of oscillations per second. This effect of heat increases until the number of oscillations per second is about four hundred billions and the wave-length is only about 750 $\mu\mu$, when the ethereal waves begin to affect our eye as light, and continue to do so till the wave-length comes down to

[1] Langley, Researches on Solar Heat, 1884, p. 72.

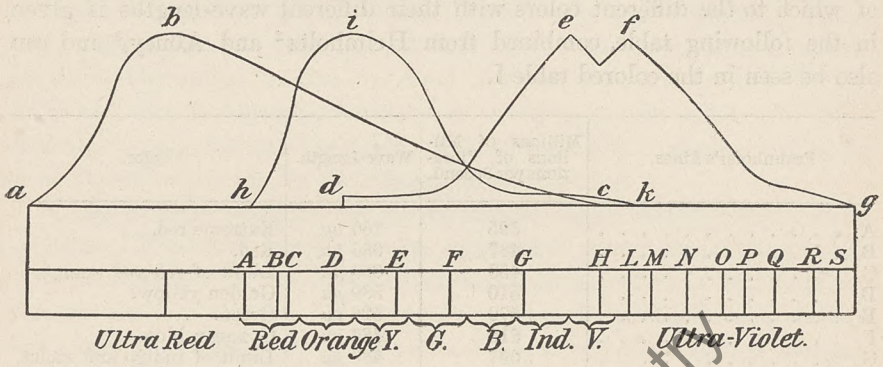
[2] The unit μ equals one-millionth of a millimetre.

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about 380 $\mu\mu$ or the number of oscillations increases to about eight hundred billions per second. Shorter waves are not perceived by our eye as light, but they show their presence by chemical effect. These actinic rays must be emitted by the sun up to the very smallest wave-length, but they do not all reach us here on the surface of the earth; for Cornu[1] could show that at an elevation of 2570 metres the sunlight contains ethereal waves of only 293 $\mu\mu$, and he found also that in the electric arc light there are waves as short as 211 $\mu\mu$ and even 156 $\mu\mu$, the latter of which disappeared at one-tenth metre from the light. We may therefore speak of *electric*, *thermic*, *photogenic*, and *actinic* rays in the ether.

Fig. 1 may serve to show the different effects of these different ether waves. Line *abc* gives the thermic curve as observed by a salt prism,

FIG. 1.



curve *hik* is that of the luminosity of the spectral colors as perceived by our eye and analyzed by a glass prism, while *defg* represents the chemical effect as found by a quartz prism. The visible ether waves reach only from *A* to *H;* at the same time we can observe how the thermic effect is not confined exclusively to the ultra-red rays, but extends over the whole visible spectrum. It is further apparent that the actinic effect is not only an exclusive property of the ultra-violet wavelets, but belongs in a smaller degree also to the luminous vibrations; indeed, Captain Abney has succeeded in finding chemical substances that are even decomposed by the ultra-red rays.

Here we have to confine ourselves to those rays that affect our sight; and we have mentioned already the rays which contain only *one* kind of wave-length (from 750 to 380 $\mu\mu$), the rays of monochromatic light. But the natural light of luminous bodies is not usually of one color. It contains in each ray waves of very many different lengths, so that we call it *mixed* or *compound* light, as each ray may be regarded as consisting of many rays of different monochromatic light. Such mixed lights we also have in the light of the sun. To prove that this is the case, we allow the

[1] Helmholtz, Handbuch der physiologischen Optik, 2d ed., p. 288.

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white sunlight, after it has passed through a narrow slit, to go through a prism which has the property of bending the different rays differently, according to the wave-length existing in each. We find then the beautiful expansion of colors that is called the *spectrum*, extending from red, the least refracted light, through orange, yellow, green, blue, to violet, which is most deflected.[1] These colors are so gradually changing one into the other that it is impossible not only to give to each color in the spectrum a certain definite breadth, but also to give names to all the different hues, of which more than one thousand could be distinguished by Aubert. But, as it has been possible to measure the wave-length of each part of the spectrum, we are always able to define a certain spectral color by saying that it must be of such and such a wave-length. We are also helped in this determination by certain dark lines in the solar spectrum,—Fraunhofer's lines,—the relation of which to the different colors with their different wave-lengths is given in the following table, combined from Helmholtz[2] and Abney,[3] and can also be seen in the colored table I.

Fraunhofer's Lines.	Millions of Millions of Vibrations per Second.	Wave-Length.	Color.
A	395	760 $\mu\mu$	Extreme red.
B	437	686 $\mu\mu$	Red.
C	458	656 $\mu\mu$	Limit of red and orange.
D	510	589 $\mu\mu$	Golden yellow.
E	570	526 $\mu\mu$	Green.
F	618	486 $\mu\mu$	Cyanean blue.
G	697	430 $\mu\mu$	Limit of indigo and violet.
H	757	396 $\mu\mu$	Limit of violet.

According to the instrumental means employed, the spectrum can be made longer or shorter. If we regard such a short spectrum in its entirety, so that the whole affects our eye, it seems to be composed of only four colors,—*red*, *green*, *blue*, and *violet*,—because by contrast with these main colors their transitions into one another disappear almost entirely; at the most, one recognizes that the green becomes somewhat yellowish towards the red. If the spectrum is made longer, the transition-colors are better recognized, but they do not make their full impression on us if the other colors affect our eye at the same time. To study each color by itself, it must be isolated by shutting off all the other colors except one, which is allowed to go through a narrow shutter. By shifting this shutter along the spectrum all the different colors can be separately studied, and it is then found that nowhere is there any sudden gap in the color-series, but that all color-tones pass into one another continuously.

[1] In this paper, as well as in that on detection of color-blindness, the spectrum has been assumed to be arranged in the usual way,—*i.e.*, red to the left and violet to the right of the observer.

[2] Physiol. Optik, 2d ed., p. 287.

[3] Color Measurement and Mixture, 1891, p. 55.

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We mentioned before that our eye is not affected by the *ultra-red* and *ultra-violet* rays. For the *ultra-red* rays, it has been proved by Brücke and Cima that the eye transmits only about nine per cent. of the heat falling upon the eye, which circumstance seems to suffice, according to Helmholtz, to explain their invisibility. It is, however, different with the *ultra-violet* rays. Donders and Rees have shown that these rays passed largely through glass vessels which were filled with vitreous fluid of the ox and into which cornea and lens had been placed. It is, therefore, not because these rays do not strike our retina that they are not perceived, but because the retina is insensible to them. From the fact that the thermic and actinic rays do not enter into our world of vision, Tyndall declared our eyes to be not perfect yet, and he hoped, from the further development of our race, that later we might be enabled to see these rays and so enjoy wonderful sights now hidden from us. Fick, however, from a teleological point of view, justly objects that the heat rays, if they should all enter our eye, would not allow our retina to rest, as these thermic rays are emitted by all bodies and even by the neighboring parts of the eye; and that, further, the ultra-violet rays, because too highly refractive, would continually disturb the acuity of our vision by their large diffusion circles.

So far we have spoken only of the simple colors furnished by a solar spectrum. These are simple because each color cannot again be decomposed by a prism, but can only be deflected. Most colors in nature, however, are not thus simple. If we put, for example, an object of a certain color, such as yellow paper, on a piece of black velvet in such a manner that the lustre is avoided as much as possible, and look at it with a glass prism of from thirty to fifty degrees, we shall find that not only does the color of the object appear, but besides, on either side, there appear colored fringes, indicating what simple colors make up the color of the object. It was observed, for example, that a piece of yellow paper, when looked at in the above manner, showed a red border on one and a green border on the other side, indicating that much red and green light was also emitted by the paper. A better way still is to hold a narrow slit in front of the pigment color and look at this with the high prism. Then nothing will be observed in the slit but the emitted elementary colors alone, which, indeed, in the case of the yellow paper were green, red, and some yellow. In such a manner the compound colors of nature can be decomposed. But this method can be also employed for a synthesis of simple colors, as may be mentioned here incidentally, especially as the books do not give it. This method consists simply in looking at two pieces of differently colored or of white paper on black velvet with a high prism, and then bringing the two pieces gradually nearer until the colored fringes partially overlap. Beautiful new colors will then appear, to be described later. One can observe this much better by looking at two narrow strips of white paper with a Browning pocket spectroscope, after having taken off the slit and the collimator lens. Each strip will then furnish a bright spectrum

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which may have an apparent length of from ten to twenty centimetres, according to the distance of the prism. This arrangement may be even used to verify roughly the table of Helmholtz, on page 587. There are various other methods of studying the effect of combining two differently colored lights. One is to allow two different simple colors of two spectra to fall upon the same place on a white screen or the same spot of the retina. Another is to make a disk, upon which two or more differently colored sectors have been arranged, rotate so rapidly that the different impressions fuse into one compound color. A third one is to look at the limit of two differently colored fields with a double-refracting prism like that contained in Javal's ophthalmometer. Then the new compound color appears in the middle between the two former color-fields. Another method is that first employed by Lambert, in which one looks obliquely through a plain glass plate at a colored surface, whilst that side of the plate which is turned to the observer at the same time sends differently colored light by reflection into his eyes. A very accurate instrument further to mix pure spectral colors and to analyze given colors like those of pigments has been described lately by Captain Abney in his book on "Color Measurement and Mixture," from which, later, a table will be given to show the composition of certain pigment colors. These methods all give reliable results, especially those that mix spectral colors; but the method of mixing solid or fluid pigments, though used by Newton, must by no means be employed.

To see this, we must consider for a little while what pigment colors are. Let us take a colored fluid. If white light passes through it, some colors in the white light are partly or wholly absorbed and some go through without being much affected by the material: it is these latter rays that give the color to the fluid. If we now mix two differently colored fluids which are chemically indifferent to each other, we can see only those colors which escape the absorptive power of both. Most blue fluids, for instance, permit the blue rays to go through unweakened; somewhat less well the green and violet; but badly the red and yellow rays. A yellow fluid, however, transmits almost all the yellow well, also red and green, but very little blue and violet. Under these circumstances it is clear that through a mixture of these two fluids the *green* rays alone will go through to a considerable degree, all the others being absorbed. The mixture will appear *green*, while a mixture of *spectral blue* and *yellow* would give *white* or *gray*. It is evident that in the two fluids there occurs no summation of the blue and yellow colors, but rather a subtraction,[1] as the yellow fluid takes away from the rays that have passed through the blue fluid all those for which it has an absorptive power. We find a similar state of affairs with regard to powdered pigments. We must regard each little particle of the pigment as a small transparent body which colors the light

[1] Helmholtz, Physiol. Optik, 2d ed., p. 314.

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by absorption; for as the light falls on it a small part of the white light is reflected from the outer part (about one-twenty-fifth on perpendicular incidence, otherwise less), but the rest of the light enters. This becomes in part absorbed, is reflected from the posterior sides of the particle, and finally after another partial absorption enters our eye as colored light. As this occurs from each little particle, we can understand how the pigment must appear colored, and how, if two such different pigments are mixed, the mixture can appear only in a light which has escaped being absorbed by both substances. So it is that blue and yellow pigments mixed give a green color like the blue and yellow fluids. This is an elementary fact to painters,[1] but nevertheless it is not true for the mixture of pure colors; because, as already mentioned in the case of blue and yellow, quite different results have been obtained by mixing the colors of the spectrum or of pigments in our eye in one of the ways before mentioned, which are all true additive processes. The results of these experiments are given by Helmholtz in the following table:[2]

	Violet.	Indigo-Blue.	Cyanean Blue.	Blue-Green.	Green.	Green-Yellow.	Yellow.
Red	Purple.	Dark rose.	Whitish rose.	White.	Whitish yellow.	Golden yellow.	Orange.
Orange	Dark rose.	Whitish rose.	White.	Whitish yellow.	Yellow.	Yellow.	
Yellow	Whitish rose.	White.	Whitish green.	Whitish green.	Green-yellow.		
Green-yellow .	White.	Whitish green.	Whitish green.	Green.			
Green	Whitish blue.	Water-blue.	Blue-green.				
Blue-green . .	Water-blue.	Water-blue.					
Cyanean blue .	Indigo-blue.						

In this table the spectral colors at the top of the vertical columns and to the left of the horizontal ones are the primary simple colors to be mixed, and the result of this mixture is indicated by that color where the corre-

[1] Painters frequently ridicule the statements of scientists about color-mixture, because they do not see the radical difference between the term color-mixture as used by physicists and the same term as used by themselves. The former mean by this term the mixture of two color-sensations, while the latter denote by it their mixture of material pigments; the first refers to the addition of two sensations in our color-perceiving mind, while the second refers to the bringing together of two colored bodies which, after their mutual incorporation, do not send the two former single colors into our eye at the same time, but only a residual one, after the combined absorptive power of the two substances has done its work on the light. One may compare the two colors entering into the physicist's color-mixture to two enemies that attack our mind together, while the two colors of the painter's mixture may be regarded as two mutual enemies who first combat each other violently before they assault our psyche with the remainder of their forces. That our mind must be differently affected under such circumstances is clear, and we may easily understand how painters and scientists differ though each is right in his own field.

[2] Physiol. Optik, 2d ed., p. 321.

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sponding horizontal and vertical columns intersect. We infer from this table that by the simultaneous effect of different simple colors on the same spot of the retina only two new colors have been produced, *purple* and *white*. Purple is obtained by the mixture of violet or blue with red, and seems to form for our eye a bridge between the red and the violet of the spectrum. And still *purple does not exist as such in nature;* there is no part of the spectrum in which the wave-length is such that the corresponding color would be purple. It is a *color-sensation* only, produced in us by the simultaneous impression of blue and of red. Here we are clearly confronted with the difference between color in a physical sense as an ethereal vibration and color in a physiological sense as a sensation, which difference we must always bear in mind. In the same sense we must call *white* a new color-sensation, which can be obtained first, of course, by combining again all the colors of the spectrum. But it has been further observed that even two simple colors, taken from different parts of the spectrum and mixed in a certain ratio, will give white. Two such colors are called complementary, a series of which is here given from Helmholtz:

Color.	Wave-Length.	Complementary Color.	Wave-Length.	Ratio of the Wave-Lengths.
Red	656 $\mu\mu$	Green-blue.	492 $\mu\mu$	1.334
Orange	607 $\mu\mu$	Blue.	489 $\mu\mu$	1.240
Golden yellow	585 $\mu\mu$	Blue.	485 $\mu\mu$	1.206
Golden yellow	573 $\mu\mu$	Blue.	482 $\mu\mu$	1.190
Yellow	567 $\mu\mu$	Indigo-blue.	464 $\mu\mu$	1.221
Yellow	564 $\mu\mu$	Indigo-blue.	461 $\mu\mu$	1.222
Green-yellow	563 $\mu\mu$	Violet.	433 $\mu\mu$	1.301

Green has no simple complementary color, but only a compound one, —purple. Later, other observers, like Von Kries, Von Frey, König, and Dieterici, have each given their table of complementary spectral colors, which on the whole agree very well, but show at the same time distinctly that there are individual differences in the normal color-perception of men, to which fact we shall return later. For the present we must state again that, as the result of the mixture of two or more homogeneous lights, except *purple* and *white*, and their transitions into the spectral colors, no new color-sensation can be produced. For each resulting sensation of the combination there exists in the spectrum a homogeneous color of a certain definite wave-length, which produces the same or nearly the same color-sensation, and every new sensation of purple and white can be referred to its spectral components.[1] That the new color is not always of the same intensity will be explained later.

We are now in a condition to remark that all possible combinations of

[1] Or, as Captain Abney expresses it in his excellent book, Color Measurement and Mixture, p. 162, "The hue and luminosity of any color, however compounded, may be registered by a reference to white light and a single ray of the spectrum." This special ray of the spectrum he calls the dominant ray, which term will be employed later in this paper.

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different luminous wave-systems of the ether lead only to a comparatively small number of different states of stimulation of the visual apparatus which appear in the different color-sensations. And in this sensation of each color we always distinguish three elements, or constants, as they are called, which are (1) *hue*, (2) *purity*, (3) *brightness*.

The first characteristic of any color is its *hue*, which tells us whether the color is red, green, blue, etc. This, in the spectral colors, depends physically, as we have seen, upon the wave-length of the ethereal vibrations in each ray, and thus we can use the two terms hue and wave-length promiscuously when we have to do with spectral colors. But we have rarely to do with spectral colors; mostly the natural colors are made up of several rays or groups of rays, and then we can compare the resulting color-sensation with the nearest spectral color of a definite wave-length, or for purple and white with the nearest combination of two spectral colors, and thus define the hue. The accurate definition of a color by reference to the spectrum is absolutely necessary for scientific experiments, but ought also to be used for an accurate description of the colors of Holmgren's wools and the colored glasses used by the railroad companies. For then alone can we always find the same colors again after fading or other deterioration. Captain Abney has done so for the red and green glasses used by the different railroads in England, and has given his observations in the report of the Committee on Color-Vision in the Proceedings of the Royal Society, July, 1892, to which we shall have occasion to refer frequently. This table is given below, and gives the wave-lengths in the spectrum of the *dominant* colors of the signals which have been adopted by some of the principal railroad companies of England, these glasses being illuminated first by an electric arc light and secondly by gas-light. The percentage of white light mixed with the spectral color is also shown, together with the luminosity of the light transmitted.

Glass.	Electric Light.			Gas-Light.		
	Dominant Wave-Length in $\mu\mu$.	Percentage of White Light in Color.	Luminosity if Naked Light equals 100.	Dominant Wave-Length in $\mu\mu$.	Percentage of White Light in Color.	Luminosity if Naked Light equals 100.
Reds.						
Great Western	625	7	10.4	627	12	13.1
Ruby Glass L. B. S. C.	620	0	10.4	620	0	13
Great Northern	625	0	9	627	0	10
Greens.						
Great Western	492	46	21.8	507	50	18.1
L. B. S. C.	492	38	16.2	505	34	12.5
Great Northern	510	61	19.2	517	62	19.4
Great Eastern	500	54	15	512	40	15
Saxby and Farmer's	492	24	7.6	505	22	6.9
District Railway	550	32	9.1	532	50	10.6

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The definition of the colors of Holmgren's test-wools will be given in the article on "Detection of Color-Blindness."

The second constant of color is *purity*, called *tint* by Maxwell. We call a color the purer the less white is mixed with it. Purity must not be confounded with brightness, for many bright colors are not pure, but contain a large admixture of white; nor must it be thought that pure colors are always strong, rich, and deep, for there are parts in the spectrum which, though of course perfectly pure, can be recognized only with difficulty. All pigments reflect also some white light, and so can never be perfectly pure, though colored papers in certain positions and colored worsteds in general may approach a pure color very nearly.

As the third constant or quality of color we must mention *luminosity*, or *brightness*, called *shade* by Maxwell. This factor depends objectively on the *vis viva* of the ether movement, and is therefore proportional to the square of the greatest velocity of the ether particles; but for us it depends not only upon the energy in the ether, but also upon the sensitiveness of our retina for the different colors. This has been shown by S. P. Langley,[1] whose table is given here:

Color.	Crimson.	Red.	Orange.	Yellow.	Green.	Blue.	Violet.
Wave-length .	750 $\mu\mu$	650 $\mu\mu$	600 $\mu\mu$	580 $\mu\mu$	530 $\mu\mu$	470 $\mu\mu$	400 $\mu\mu$
Luminosity . .	1	1,200	14,000	28,000	100,000	62,000	1,600

Unity in the third horizontal line is the amount of energy required to make us see light in the extreme red end of the spectrum near Fraunhofer's line A, and the higher numbers in this line indicate what visual effect the same amount of energy produces in the respective colors: so that, for example, the green near 530 $\mu\mu$ has about one hundred thousand times more visual effect upon our eye than has the crimson.

If, however, we determine the luminosity of the spectral colors directly by comparing the intensities of the shadows thrown by a pencil in these different lights, as has been done by Captain Abney (*loc. cit.*), we get the following results:

Fraunhofer's Line.	Color.	Luminosity.	
		Normal Eye.	Red-Blind Eye.
A	Dark red.	. .	. .
B	Red (crimson).	1	0
Red lithium	Red (crimson).	8.5	0.5
C	Red (scarlet).	20.6	2.1
D	Orange.	98.5	53
E	Green.	50	49
F	Blue-green.	7	7
Blue lithium	Blue.	1.9	1.9
G	Violet.	0.6	0.6
H	Faint lavender.	. .	. .

[1] Energy and Vision, National Academy of Sciences, vol. v., First Memoir, 1888.

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Here we see that the greatest luminosity exists in the orange-yellow near line D. The fourth vertical column shows the luminosity of the same spectral colors to a red-blind eye, and will be referred to again later. Of course not only the spectral but also the pigment colors differ in luminosity, as is shown in the following table from Captain Abney, in which the luminosity of these pigments in electric light is determined when that of white paper under the same conditions is equal to 100:

Pigment Color.	Luminosity in Electric Light.
White	100
Vermilion	36
Emerald green	30
Ultramarine	4.4
Orange	39.1
Black	3.4
Black (different surface)	5.1

Having thus obtained a clear conception of the three color-constants, we are now in a position to define exactly any color by its hue (comparing it with a spectral color or a combination of them), its purity or tint (absence of white light entering into it), and its brightness or shade (the amount of energy in it for our eye or the amount of black being mixed with it). But, instead of doing it by these three variable quantities, a color may be also defined as a mixture of variable quantities of three colors, the so-called primary colors, as which formerly *red*, *yellow*, and *blue* were regarded. If one should take this doctrine objectively, as if there were three objective simple colors in the spectrum, by the combination of which there might be produced the same impression upon the eye as by any other simple or compound light, he would be quite wrong. There are no three simple colors in the spectrum, as Brewster thought, by the combination of which the intermediate colors of the spectrum could be constructed. These intermediate colors always appear much more saturated in the spectrum, even if one takes a much better selection for the three primary colors,—namely, *violet*, *green*, and *red*. Then, indeed, one may from red and green obtain yellow; but this is by no means like the brilliant color of the spectrum. The reason for this, as will be given more in detail later, is that even the spectral colors, though the purest in nature, excite in us not pure color-sensations alone, but some white also.

At present we must conclude from the foregoing facts that it is not necessary to assume as many primary color-sensations in us as there are innumerable colors in the spectrum and combinations of them. We may reduce them very much. Two color-sensations will not suffice, but by the help of three we can produce all the color-sensations that the spectrum can give. This fact has given origin to different theories of color-perception, a few of which will be described later. Before doing that we must refresh

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the reader's memory about some important facts of the physiology of the nerves, as this will assist him very much to judge about these theories.

When a stimulus is applied to a nerve a peculiar change occurs in it, which manifests itself in the motor nerve by the contraction of a muscle and by a sensation in the sensory nerve. The most important peculiarity about the two kinds of nerves is that, in the words of Helmholtz, "so far no difference in the structure and function of the sensory and motor fibres is known which could not be derived from their different connections with other organic systems. The fibres themselves seem to play only the part of indifferent conducting fibres, which work as motor or sensory nerves, according to whether they are connected with a muscle or a sensitive part of the brain."[1] Another important fact is "that by the stimulation of every sensory nerve-fibre only such sensations arise as belong to the region of the special sense, and that every stimulus which is able to excite the nerve-fibre, be it mechanical, chemical, electrical, etc., produces only sensations of this special character."[2] This is well shown by a sudden blow on the eye, which produces a suddenly appearing and disappearing, often very bright, light-sensation over the whole visual field. If, in a man, the eyeball is extirpated and the optic nerve not yet disorganized, great masses of light appear at the moment the nerve is being cut. That, according to Foster, this has not been observed always may easily be explained either by the nerve being in a pathological non-excitable condition or by the excitement and pain which arise from the cutting of the numerous small nervi nervorum, and which may easily overpower the light-sensation in the consciousness of many a patient. That the rough blow or the cutting of the nerve can compare with the subtle ethereal wavelets nobody will assert, and yet they produce the same effect. Again, if light strikes the retina we know that we see it only after it has reached the layer of rods and cones. These latter are struck by the ethereal impulse of from four hundred to eight hundred billion times per second. It is impossible that the cones and rods should vibrate in unison with the ether particles,[3] for then they either would simply burn up or would show the phenomena of fluorescence or phosphorescence, which have never been observed, at least in the macula. Such fluorescence would further mean that the actinic rays which produce this most strongly ought to be most powerful on our retina, whilst we know that the retina is not sensitive to them. It is, therefore, necessary to assume that it is a different change that is going on in the nerve and in the ultimate elements of the retina. What occurs, very likely, may be compared, with Clifford,[4] to what happens in a train of gunpowder. All the molecules here are in a state of unstable equilibrium, and a spark

[1] Helmholtz, loc. cit., p. 232. [2] Ibid., p. 233.

[3] As the Committee on Color-Vision remarks, p. 303, "It is difficult to conceive that matter which is so comparatively gross as the rods and cones which are situated on the retina can be affected by the merely mechanical action of the vibrations of light."

[4] Seeing and Thinking.

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to one end will upset this equilibrium there; the molecules changing their positions and entering into new combinations will cause the next particles to do the same, until finally all the molecules are again in equilibrium and the powder is burnt.

This is a chemical process, and in a similar way we must imagine that the ether molecules set energy free in the rods and cones, producing a chemical decomposition there as they do in the sensitive plate of the photographer, which molecular change travels up the nerve to the brain. From what has been already said about the identity of all nerve-fibres, it is most probable that the nerves are capable of only one kind of chemical change, so that the most unlike stimuli to the optic nerve produce the same effect of a chemical decomposition in it; just as a drop of nitro-glycerin becomes decomposed in the same manner whether the hammer or the thermic ether-waves strike it. And if that is so, if there is no vibratory but only a chemical change of the same kind in all nerve-fibres, whatever stimulus is applied, whether a blow or colored light, it is evident that we have to drop all theories which suppose that each fibre can conduct different vibratory changes when it is stimulated by different colors; we have to give up the idea, advanced by Prince Kropotkin, "of different undulations travelling along the nerves and being the source of different sensations."[1] Such a theory has also been broached in a very learned essay by Dr. Swan M. Burnett,[2] which ought to be fully discussed if space allowed it. His theory, too, makes the same nerve the conducting apparatus for different colors, so that the brain is made the differentiating organ and the nerve-fibre is supposed to undergo different changes, according to the different colors striking the terminal. But there is another fact, in addition to those from the physiology of nerves, which makes it very probable that the retina is the differentiating or sifting organ. There are well-authenticated cases of *uniocular* color-blindness which can be explained only by an ante-commissural defect, which, from the fact that the visual acuity is not reduced, must most probably be placed in the retina. As Professor Rutherford[3] says, "By some it is believed that congenital color-defect is due to the brain. If there had been defective color-sense on one side of the brain, it would not have implicated the whole of one eye, but the half of each eye. Its limitation to one eye, therefore, seems to me to suggest that the fault was in the eye rather than in the brain." And if that is so, then we would seem to be justified in assuming from this fact alone that the retina is also the differentiating organ in normal color-perception, because when it is at fault the remaining parts of our visual apparatus are not able to distinguish the colors normally. Oliver, in the *American Journal of the Medical Sciences*

[1] Recent Science, in August number (1893) of Nineteenth Century.
[2] American Journal of the Medical Sciences, July, 1884.
[3] Our Sense of Color. Opening presidential address, Section D, Biology, British Association, 1892.

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for 1885, gives, in a very elaborate article, "a correlation theory of color-perception," in which he states that "each and every healthy optic-nerve filament transmits to the color-centre for recognition nerve-energies equal to as many special sensations as its peripheral tip is capable of receiving," and that "color-perception takes place through each and every optic-nerve filament." But against such a theory the words of Donders[1] may be cited: "Moreover, more than one process in the same form element [of the retina] would have supposed more than one process of conduction in the corresponding fibre, against which physiology wishes to put in its veto."[2] Oliver justly lays great stress on a comparison with the sense of touch, and says, "It would be foolish to assert that there may be special divisions of peripheral tactile nerves especially adapted for the three empirical sensory impressions,—cold, warm and hot," etc. But has it not been proved by the researches of Goldscheider that there are special nerve-endings for heat, cold, pain, and touch? It seems that this reference to the skin ought to strengthen the theory which is here proposed and which agrees well with the "law of specific energy."

These facts narrow down considerably the region for possible color-theories, which will be further reduced by another consideration, given by Helmholtz[3] as follows: "For the motor nerve we know only the antagonism between the state of rest and that of activity. In the first state the nerve can be left unchanged for a long time without considerable metabolism or development of heat; hereby the muscle connected with this nerve remains limp. If the nerve is stimulated, there is developed heat in it, material change, electric oscillations can be demonstrated, the muscle contracts. In the dissected muscle preparation the conductivity is soon lost on account of the consumption of those chemical constituents that are necessary for activity. Under the effect of atmospheric oxygen, or, better still, of the arterial blood containing oxygen, the irritability is slowly reproduced, wholly or partly, without these assimilative processes producing any contraction in the muscle, or without giving rise to changes in the electric behavior of muscle and nerve accompanying their activity. Further, we know no outer means which could excite the assimilative process so rapidly or intensely and could initiate or stop it so suddenly as would

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[1] Arch. für Ophthalmol., xxvii. 1, p. 173.

[2] This must also be urged against a new theory lately proposed by Chr. L. Franklin. Her articles upon this subject in Mind, New Series, vol. ii., 1893, Zeitschr. f. Psych. u. Physiol. der Sinnesorgane, Bd. iv., etc., are, nevertheless, of profound interest and ought to be carefully perused by the student of this field of physiological optics. Quite in agreement, however, with this physiological law, a new theory has been lately propounded by Dr. J. Wallace, who tries to establish a definite relation between the length of a cone and the color acting on it. Mauthner, in his Farbenlehre, 1894, refers to it as an important contribution to the subject. But according to this theory each cone ought to have always the same length, which does not seem to be the fact, according to Stort (Akad. zu Amsterdam, June, 1884).

[3] Loc. cit., p. 349.

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be necessary if this process should serve as a physiological foundation of vivid and regularly starting sensations." Now, as we have every reason to believe that the sensory nerves possess the same properties as the motor nerves, it must be clear that all theories which make this process of assimilation as active as that of dissimilation for our sensations are in direct antagonism with the best-established facts of our nerve physiology. This is done by Hering in his color-theory, of which we shall speak more hereafter.

We shall now give a theory of color-perception which dates back to the beginning of this century, and was in its rudiments then given by Thomas Young. This was later taken up by Helmholtz and made the basis for explanations in the first edition of his celebrated "Physiologische Optik." We shall not enter into the historical development of this theory, but shall simply state it in its latest modified and improved form as given in the second edition of Helmholtz's book, which is now being published. Helmholtz has made some important additions, with regard to which he modestly remarks on page 349, "That objections to these additions do not refute Young's hypothesis (of three primary color-sensations) I need not, of course, explain any further."

1. In the eye are three kinds of nerve-fibres, all identical in their structure and conducting processes, but supplied with different end-organs (rods and cones). One kind of end-organs we will call the red-perceiving or *red-sensitive* end-organs, because they are supplied with a photo-chemical substance which is mostly affected by the red rays of the spectrum, though the other rays affect it also to some extent. The second kind of end-organs, the *green-sensitive*, are endowed with a photo-chemical substance mostly sensitive to green light; and the third kind of fibres, the *blue-sensitive*,[1] with a third substance mostly sensitive to blue.

2. By the decomposition of each of the sensitive photo-chemical substances the fibre connected with it is stimulated. There is only one kind of sensation-producing activity in each nerve-fibre, which is accompanied by decomposition of the organic substance and development of heat in the same way as we know it to be in the muscle-nerves. These processes in the three fibre-systems are, therefore, probably of entirely the same character, and they affect us differently only because they are connected with functionally different parts of the brain. The nerve-fibres need play only the part of electric wires, which are traversed by the same electric current and yet may produce the most different results, according to the instruments with which they are connected. These stimulations of the three fibre-systems play the *rôle* of three elementary stimulations, provided that the strength of the stimulation, for which as yet we have no general measure, is put down as proportional to the strength of the light. This proportionality does not prevent us from assuming that the intensity of the

[1] Helmholtz speaks usually of violet sensitive fibres, but, as he himself later inclines to blue, this has been selected here.

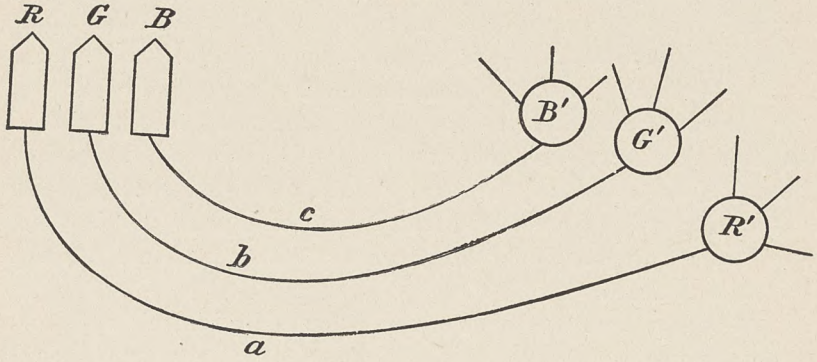
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elementary stimulation may be any complex function of the metabolism or the negative variation in the nerve.

3. In the brain these three fibre-systems are connected with three functionally different systems of ganglion-cells, which perhaps are locally so placed to each other that those are near together which correspond to the same retinal area.

A little diagram, perhaps, will serve to make this somewhat plainer.

FIG. 2.



In Fig. 2, *abc* are the identical nerve-fibres. *R* is the red-sensitive end-organ of *a*, *G* the green-sensitive of *b*, and *B* the blue-sensitive of *c*. *R′*, *G′*, *B′* are the three brain-cells, probably in the cuneus, whose specific energy is for us identical with a sensation of red or green or blue, no matter in what way that energy has been aroused, whether by the usual way of the nerve or by central irritation in the brain, as in sleep. We see that this theory makes the retina only the differentiating or selecting organ, while the brain alone is the perceiving one. With regard to the three different photo-chemical substances, it must be admitted that at present they are only hypothetical; but as we have already found one substance in the retina that is very sensitive to light,—the visual purple, which was discovered only a few years ago, in 1876,—we may well suppose that there are other chemical substances yet to be discovered by actual experiment.[1] Perhaps we may then, indeed, find that the visual purple itself plays a very important part in color-vision, as has been suggested lately by Ebbinghaus, but that can be decided only by further investigations. Later we shall get some idea about the relation of the three photo-chemical substances to each other.

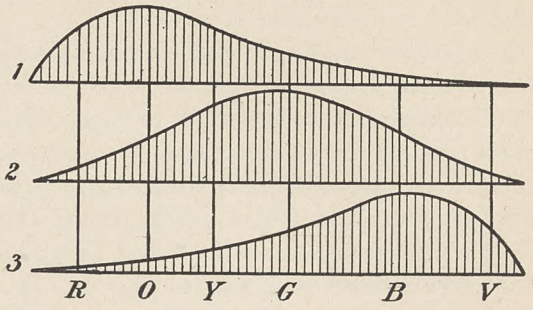
At present we must see in what way these three chemical substances are affected by the different spectral colors. The diagram on the opposite page may serve to show this in a rough way.

[1] Kühne, in Hermann's Handbuch der Physiologie, p. 341, is of the same opinion when in his article "Chemische Vorgänge in der Netzhaut" he remarks that "everything urges us to assume also colorless visual substances in the visual cells."

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Here the spectral colors must be imagined to be placed at the letters *R O Y G B V*. Then the three curves may represent the amount of stimulation that is given to each substance by the different spectral colors, No. 1 being for the red-sensitive, No. 2 for the green-sensitive, and No. 3 for the blue-sensitive substance.

FIG. 3.



The spectral color *red* stimulates strongly the red-sensitive substance, less the green, and least the blue one. Sensation equals *red*.

The simple *yellow* excites moderately the red- and the green-sensitive material, little the blue. Sensation equals *yellow*.

The simple *green* excites strongly the green-sensitive, but less the other two substances. Sensation equals *green*.

The simple *blue* excites strongly the blue-sensitive, little the red- and the green-sensitive material. Sensation equals *blue*.

The simple *violet* excites strongly the blue-, less the green- and the red-sensitive substance. Sensation equals *violet*.

Stimulation of all the three substances to about the same degree gives the sensation of white or of very whitish colors. We see here that every spectral color stimulates all the substances more or less, so that really the spectral colors do not represent the pure sensations. To obtain these we are obliged to have recourse to an artifice, which will be mentioned later. Helmholtz has lately calculated, from very careful experiments performed by König and Dieterici as well as by Brodhun, what must be the primary color-sensations if Weber-Fechner's law[1] is assumed to have not been violated in those observations. He found that *carmine red*, the *green* of *vegetation*, and *ultramarine blue* are nearest to our primary sensations. He also found[2] "that all simple colors stimulate all the light-sensitive nervous elements of the trichromic eye simultaneously and with only moderate differences of intensity. If we, therefore, hypothetically reduce the stimulation to the presence of three photo-chemically changeable substances in the retina, we must conclude that all these three have nearly equal limits of light-sensitiveness, and that they show only secondary deviations of moderate amount in the curve of the photo-chemical effect for the different

[1] This law states that within certain limits the increase dE in our sensation E is directly proportional to the increase of the stimulus dH, and inversely proportional to the stimulus H; or mathematically dE equals $A\frac{dH}{H}$, where A is a constant.

[2] Loc. cit., p. 457.

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wave-lengths. Similar changes by admixture of other substances, substitution of analogous groups of atoms, etc., occur in other photo-chemically changeable substances as they are used in photography,—for example, in the different haloid salts of silver."

Objections to this Theory.—Helmholtz's theory supposes that each terminal element has its separate nerve-fibre; but this cannot be, as Salzer found that there are about three millions of cones alone in the human retina, while the optic nerve cannot have more than one million fibres. This objection, however, is not valid; for though we must assume one separate fibre for each cone in the fovea centralis, there is no necessity of doing the same for the peripheral parts of the retina. On the contrary, Helmholtz himself has given a theory which shows how the facts of peripheral vision can be explained much better by the assumption that many nervous end-elements are connected with one fibre alone.[1]

Another objection—raised by Fick years ago—has been lately brought forward by Professor Rutherford in his opening presidential address to Section D, Biology, in the British Association. He says that according to Helmholtz's theory a colorless small pencil of light—as from a star—ought not to be seen without a color unless it fall on three cones at the same time, which, from astronomical observations, is not the case. And, indeed, this seems to be a fact fatal to the theory; because we see the white star white, and know that its image, on account of its small size, can cover only one cone. But it only seems so; for we must not forget that our eye is continually going through very small movements, which, leaving out of consideration other factors, have their principal cause, perhaps, in the rhythmical innervation of the muscles that hold the eye fixed. The distance between two cones in the fovea is at the most 0.008 millimetre, corresponding to an angle of about 2′ measured from the second nodal point of the eye. Now, if the eye in these small oscillations moved through an angle of only 2′, this movement in all directions would bring the point of light on the retina in relation with at least seven different cones. The cornea would move through a circle of only 0.0075 millimetre radius, which cannot be observed with the naked eye. We see, therefore, how small a movement of the eye suffices to expose very many little cones, one after another, to the same point of light, so that the brain can easily perceive, by a quick comparison of the impressions obtained successively by the three color-cells R', G', B' (Fig. 2), whether the light from the distant star is white or colored. For if all the cells are excited to the same degree, rapidly, one after the other, we judge the star to be white; but if, for example, the R' cell gets the strongest impression comparatively, we call the star or point of light red.[2] This explanation will also give an

[1] Loc. cit., p. 264.

[2] This explanation of the difficult question is not given by Helmholtz, but is brought forward here for the first time, so far as known to the writers.

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answer to the following passage from Rutherford's lecture: "Whichever view [whether light stimulates the optic terminals by inducing vibrations or by setting up chemical changes] we adopt, it seems to me necessary to suppose that all the processes for the production of nerve-impulses can take place in one and the same visual cell, and are transmitted to the brain through the same nerve-fibre, because the image of a colored star small enough to fall only upon one cone is seen of a fixed and definite color, which does not alter when the position of the eye is changed. It seems to me that if there are special cones for red, green, and blue, the color of the star should change when its image falls on different terminals; but I am assured by Lockyer that such is not the case." It seems that in this regard the retina may be compared to the skin. Here also we find different end-elements, one sensitive to pressure, another to heat, and still another to cold; so that only by exposing different parts of the skin to very small objects do we find out these properties.

Another objection raised by Fick is the following. Every ray of light, while exciting a color-sensation if it fall on a sufficient area of the posterior polar part of the eye, provided it acts on an extremely limited part of the retina, even if it be colored light, produces a whitish impression. This is exactly the opposite of what we should expect,—viz., the smaller the area of the retina acted on, the more easily should the peculiar nerve-ending be excited and a pure color-sensation result. Here it is to be replied that this is true only if the amount of light falling to the "extremely limited part" is small, because we really do see distant stars colored. And the reason why we see the small amount of colored light whitish depends upon the fact that with weak light the curves for the sensitiveness of the three photo-chemical substances to the different colors almost coincide, so that in our brain the three different color-perceiving cells are stimulated to about the same degree, giving the whitish sensation. If, however, the retinal area of the same dim colored light be greater, then more color-perceiving cells are stimulated, and the small difference in their stimulation may then become large enough to enter the threshold of consciousness: we see again color.

A. Charpentier[1] objects to the Young-Helmholtz theory because it does not explain the fact, proved by him, that even the central parts of the retina are less sensitive to color than to white light. But it seems that this theory can account for it very easily, because it assumes that white light stimulates all the three cones equally, so that now three brain-cells are excited, while by monochromatic light only one cell is considerably aroused.

The great majority of human eyes belong with regard to color-perception to one and the same class. As three colors, or, more correctly expressed, three primary color-sensations, are required to explain their color-perception, these eyes are called *normal trichromic eyes.* But the

[1] Cited by Prince Kropotkin in his article before mentioned.

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three primary sensations are not always exactly alike in different men, or even in the two eyes of the same observer. This has been already mentioned in the case of different persons, and is also shown for the same individual in the observations with the leukoscope[1] of Helmholtz, in which instrument one endeavors to make two complementary colors produced by quartz plates in polarized light as equal as possible to each other; and as a coloring of the media of the eye sufficient to explain this phenomenon has never been observed, we are driven to the assumption that even in normal trichromic eyes the intensity of the stimulation of each primary color-sensation is a function of the wave-length of the light, slightly different in different individuals. But all those persons who can distinguish all the colors of the spectrum must be called normal with regard to color-perception. There are, however, persons—the so-called *color-blind*—who do not see all the colors in the spectrum. Some, indeed, —the so-called achromatics or monochromatics,—see no different colors at all there, but only different shades. Such cases are very rare.[2] More frequently we find people who can see only two colors in the whole spectrum. They are called dichromatics, and the study of their defect is of great practical importance to the employees of railroad and navigation companies.

In general there are two kinds of dichromatics. If the spectrum is shown to the first kind, they will say that red, orange, and yellow are all yellow, red being described as dark yellow, orange as less dark, and yellow as bright yellow, whilst the green part of the spectrum bordering on the yellow will be described as yellow diluted with white. In the normal blue-green they point out a white or gray band, the so-called neutral band; the blue near it they describe as a whitish blue, whilst the rest of the blue appears light blue and the violet dark blue. (See Plate, vol. ii., article "Color-Blindness." If they are given certain light green and dark red worsteds, they will often not see the difference in hue. They cannot always distinguish a dark-green pattern on a black background, but they can see well a red one on the same ground. The spectrum is not shortened for them at the red end, and the maximum of intensity is for them in the yellow. As the neutral line is in the green, we must assume that these persons do not perceive the green as we do, and they are for that reason called *green-blind*. Purple, which, as we know, excites a blue and a red sensation, the green-blind can distinguish from blue, as both colors excite in him the corresponding sensations; but he confounds it with green and gray.

This is not so in the second class. Here the individuals cannot distinguish purple from blue. The spectrum appears shortened to them, as is well shown by Captain Abney's table on page 608; it begins usually in the orange, and, as they do not see the extreme red, they are called *red-blind*.

[1] Diro Kitato, Zur Farbenlehre, Dissertation, Göttingen, 1878; A. König, Wiedemann's Annalen, Bd. xvii., 1882; Helmholtz, Physiol. Opt., p. 372.

[2] To obtain some idea of the way in which the different colors appear to them, vide photograph of Thomson's color-stick, in article on Color-Blindness.

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To them the spectrum also consists of only two colors, yellow and blue, but the neutral white or gray line lies in the green-blue, more towards the blue than in the first class; they have their maximum of brightness in the spectrum also more towards the blue, in the yellow-green. They frequently confound light red with dark green.[1]

That both these classes of dichromatics can mix all the colors by *yellow* and *blue* was shown by Donders,[2] who made two different color-blind persons copy a color-circle containing one hundred different colors with these two colors alone. Each regarded his copy as perfect, but ridiculed that of the other. Now, how does the Young-Helmholtz theory explain the color-perception of the color-blind? Formerly, Young and Helmholtz explained these defects by assuming an entire absence of the red- or green-sensitive fibres; but lately, in the second edition of the "Physiologische Optik," Helmholtz has given an explanation that seems to be more probable. We have seen that he assumes three photo-chemical substances which are comparatively only slightly different, and which for brevity's sake may be called the red-, green-, and blue-sensitive substances. He further assumes that in normal eyes there is such a genetic relation between the red- and green-sensitive substances that the green one in some cones is further developed into the red one.[3] Now, in those persons who are called green-blind this normal metabolism is perverted. All those cones which in the normal eye carry the green-sensitive substance have this latter also developed at once into the red-sensitive substance, so that there exist then only cones with red-sensitive and blue-sensitive material. In other words, looking back to Fig. 2, G has become equal to R, while all the rest—the fibres a, b, c, and the brain-cells R', G', B'—remain the same. If now red light strikes the cones, all these R cones are affected, thus, however, stimulating both R' and G' cells of the brain. But if in the normal eye R' and G' are equally aroused, as is done by the yellow of the spectrum, it has the sensation of yellow. This same spectral yellow affects now in our green-blind person all the R cones, and therefore the G' and R' cells, equally, so that yellow must make the same impression upon his brain as in the normal eye, if we suppose with Helmholtz that the brain-cells do not differ much in either case. Further, as the spectral red also arouses the cerebral R' and G', it is clear that the patient cannot distinguish between yellow and red, both affecting his brain in almost the same manner. He will call the red yellow, and it is evident that all his color-sensations will be com-

[1] It must be confessed that there is a great deal of difference in different authors in the description of the manner in which the color-blind see. The present description, however, is given by the best observers, and borne out, at least for the green-blind, by persons with *uniocular* green-blindness and by the careful self-observations of Dr. W. Pole.

[2] Arch. für Ophthalm., xxvii. 155 *et seq.*, 1881.

[3] It would seem that, judging by the fact that the green is usually first lost in pathological cases, the green-sensitive material might be developed from the red one. But, however this may be, that would not change the following explanation.

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posed of a yellow and a blue sensation. That our green-blind individual does not see the spectrum shortened can, of course, be easily explained by the fact that his cones are red-sensitive. To explain the neutral band, we must remember that in the green, where they see this band, the red and blue cones are stimulated about equally (as Fig. 3 shows), and that therefore in our case all the three brain-cells R', G', B' are aroused to about the same degree. Now, whenever in normal or color-blind eyes all three brain-cells are equally stimulated, the sensation of white or, on equal feeble stimulation, of gray must arise. Thus we see that there must be a neutral band of white or gray in the spectrum of the green-blind, that purple, green, and gray cannot be distinguished by their *hues;* and we observe further that he must see white very much as we see it, because white light (the red and blue parts of it) excites his R', G', B' cells equally. Thus the objection is answered that is often made to this theory,—namely, that it does not explain how the red- or green-blind can see white. This explanation also does away with another difficulty which is well stated by Berry,[1] thus: "In the first place, there can be no doubt that an individual who is blind for one particular hue is at the same time blind for its complement. That this is the case is shown by the following facts. It is possible by the rapid rotation of a disk to obtain from three or more suitably selected colored sectors an impression which is identical with that of a mixture of black and white produced in the same way; the colors taken in certain proportions can be got to neutralize each other, so that the resulting impression is colorless. The slightest removal of any portion of one of the colors entering into the combination can at once be detected, and some color-sensation is the result. If, on the other hand, the disk should contain two sectors of exactly complementary colors, their simultaneous removal does not destroy the colorless effect; the remaining colors continue to neutralize each other, so that the impressions they give rise to, following each other in rapid succession, resolve themselves into gray. Now, it is found that the same mixture which to a normal individual appears similar to a mixture of black and white also appears so to the color-blind individual, whence it follows, as they are known to be blind for one color, that they must either be insensitive to two complementary hues in both disks or to only one in each. If they only fail to perceive one, both disks must appear to them colored; but this is extremely unlikely, because then all objects which appear to the normal eye colorless must appear to them colored."

The facts are here stated well, but it must be remarked that the expression "blind for one color" is misleading, as, for instance, the green-blind is somewhat affected in his eyes by the green rays of the spectrum, because the red- and blue-sensitive substances are still, though very moderately, excited; but the effect is (1) much weaker than in the normal eye and (2) differently distributed to the brain-cells, so that a different sensation must result.

[1] Diseases of the Eye, p. 336.

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Suppose, for example, that the revolving disk contained, besides other complementary hues, green and purple sectors. This to our green-blind must appear gray, just as to the normal eye; for though his eye has no green-sensitive material, still the green does affect moderately both his other photo-chemical substances, and so gives gray, while the purple affects also all his cones—the red- and blue-sensitive ones—and, therefore, all the R', G', B' cells, thereby giving likewise the sensation of gray or white. From this it follows that neither the removal of the green sector alone nor that of the purple one can change the former sensation of gray, though he is by no means blind to the red and blue color of which the purple is composed.

With regard to the other class of color-blind people, the so-called *red-blind*, the theory supposes that the change of the green-sensitive into the red-sensitive substance, which normally always takes place in a certain number of cones, does not occur at all here; so that, besides the blue-, only the green-sensitive substance exists in such eyes. In other words, the R cones have become equal to the G cones, whilst the rest of the visual apparatus remains the same. Here, also, yellow must be seen as yellow, for this color stimulates all the G cones, and, therefore, all the G' and R' cells, as yellow does in the normal eye. For the same reason green alone must be seen as yellow, or at least make the same cerebral impression as yellow. In short, we have almost the same state of affairs as in the green-blind, with the following exception. The spectrum must appear shortened to the red-blind, especially in dim light, as the red rays stimulate the green-sensitive substance only very slightly. The neutral band and the greatest brightness of the spectrum are displaced farther towards the blue, because the eye is sensitive to green. Purple stimulates much their blue- but hardly their green-sensitive substance, so that purple to the red-blind must appear blue or violet, whilst the green-blind, as we have seen, confuses gray or green with purple.

These two classes of color-blind, the *red-blind* and the *green-blind*, are often comprehended in one group,—namely, that of *red-green* blindness,—especially by the adherents of Hering's theory. And indeed it must be admitted that the persons who cannot see green as we do cannot see red either in the same way that we see this color. As Dr. W. Pole, himself a green-blind, in his latest contribution[1] to the subject, remarks, "The true solution is that I am blind to both colors" (red and green). This fact has had special stress laid upon it in this paper in order that the reader might not get the impression that the term green-blindness signified a condition in which the individual could not see green, but in which he could see red, as it is perceived in the normal eye. The terms red-blindness and green-blindness are simply retained here to give precision to the clinical difference in the two classes of red-green blind, and to give at the same time a clue to

[1] On the Present State of Knowledge and Opinion in Regard to Color-Blindness. Transactions of the Royal Society of Edinburgh, vol. xxxvii., Part II., September, 1893, p. 459.

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the etiology according to Helmholtz's theory. The old view of the entire absence of the red or green fibres has, of course, been abandoned.

There still exists a third class of color-blind, the so-called *blue-blind.* Here the blue-sensitive substance has changed its character, it having become either equal to the red- or equal to the green-sensitive material. If the B cones become equal to the G cones, the spectrum must appear more or less shortened; the red is well recognized, but the blue and green are not distinguished, as seems to have been the case with the five blue-blind patients of Magnus. In Cohn's five cases the spectral yellow was confounded with gray, because in these patients yellow excites all their cones (the R and G ones), which excites all the R', G', B' cells, thus producing the same cerebral effect that gray does. If, however, the B cones become equal to the R cones, then the patient will confound strong blue and weak red, which appears to have been the case in the patient reported by Stilling (*Centralblatt für prakt. Augenheilkunde,* ii. 99, May, 1878). Blue-blindness, on the whole, is a very rare condition, and has, therefore, not been studied very thoroughly, especially as, further, it is not of much practical importance.

A priori we might expect many more classes of color-blindness. Indeed, twenty-seven combinations of the three photo-chemical substances into sets of three would be possible, which, as only one set could be the right one, would give us twenty-six classes of color-blindness. But it lies in the nature of things that all these twenty-six combinations are not equally likely to occur, because these substances bear a certain genetic relation to each other, so that certain combinations will be very improbable and even impossible. Indeed, except one class, still to be mentioned, the three classes just given seem to cover the ground pretty well, though the "surprising multiplicity of the individual deviations" (Geissler) from the general types might sometimes have to be referred to a different combination.

The fourth class of color-blind people are the *totally color-blind,* to whom the spectrum appears perfectly achromatic. Yellow, or mostly the green, appears as the brightest gray, from which towards both ends the spectrum becomes gradually darker till it finally becomes almost black. Foster believes that such a case, well authenticated, would furnish a complete refutation of the Young-Helmholtz theory; but the vision of achromatics may be easily explained by assuming that the three photo-chemical substances have all become alike the green-sensitive substance. Green must be taken because the greatest luminosity in their spectrum is usually not in the line D (yellow), as in the normal eye, but in the green of the line E. It is here of great interest to remark that in a very dim light and after prolonged stay in darkness the normal eye sees the spectrum in the same way as is done by the achromatic, and with the greatest brightness near the line E. That the normal eye sees the spectrum gray under these conditions is explained by Helmholtz as follows. Every spectral color stimulates all the three different cones, only in slightly different strengths; but in

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order that these objective differences in the amount of stimulation may enter our consciousness and thus produce color-vision, it is necessary that they overstep certain amounts, the so-called *threshold values*. If this is not so, as in a dim illumination, we perceive only the stimulation of all the corresponding cerebral cells; we see *gray*. The displacement of the site of the greatest luminosity towards the blue must be explained by reference to Purkinje's phenomenon, according to which our eye in a very dim light is much more sensitive to blue than in a strong illumination. Although this explanation seems so natural if we accept this new theory of Helmholtz, still this phenomenon has been made the starting-point of a controversy against the Young-Helmholtz theory by Professor Ebbinghaus.[1] He admits, however, that if we make the above assumption of all the photo-chemical substances having become equal and more or less like the green-sensitive substance, at least in so far that the new substance has its maximum of intensity in that color, the observed phenomenon can be explained. But he then urges the following difficulty. If a spectrum of mean intensity is gradually darkened while the eye views the whole extent of it, then the yellow and cyanean blue disappear gradually, until finally only red, green, and violet blue remain. If the dimness increases, then green first loses its color and changes into gray; the same occurs later at the spaces where formerly the yellow and blue were seen; only the red retains its color very long. But here we must bear in mind that under these conditions we have to do with a very complicated process,—namely, with the positive after-effect of colors on and fatigue of the retina, which phenomena follow different laws for different colors, as we shall see later. It must, however, be observed in this connection that W. von Bezold and later E. Brücke concluded, from the fact that in a very short and not too bright spectrum only red, green, and violet blue are distinguished, that these three colors must be the physiological primary colors, inasmuch as they regard those elements of a mixed sensation which do not trespass the threshold of stimulation (Reizschwelle) as ineffectual also in the mixed sensation. This phenomenon, then, offers no argument against the Young-Helmholtz theory.

But here must be mentioned another fact that has been used against this theory. It is this: all simple colors, if of very high intensity, produce a whitish sensation. This fact may be explained in two ways; but from the other experience, that in a spectrum of great brightness the colors are first reduced to yellow and blue, we may assume that in an intense light the cones of a special color become exhausted of their differentiating material, so much so that their further stimulation is only slightly different from that of the other two kinds, so that all the three cones and therefore all the three brain-cells for one retinal area are equally stimulated, thus producing the impression of white. Thus, there is no difficulty for the

[1] Zeitschrift für Psychologie und Physiologie der Sinnesorgane, Bd. v. Heft 3, p. 149.

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Young-Helmholtz theory, if we only remember that these three photo-chemical substances must not be regarded as fixed constant elements like three chemical atoms, but as three genetically related substances which may change their mutual relations under certain circumstances.

Color-Vision in the Peripheral Parts of our Retina.—Deviations from normal color-vision similar to those observed in the color-blind occur also in the peripheral part of the normal retina. We do not recognize the color of an object at the very extreme part of our field of vision; everything makes the impression of gray. Farther towards the middle of the visual field the difference between blue and yellow is first recognized, though blue is usually seen a little more peripherally. In this yellow-blue zone deep red appears almost dark or dark yellow, blue and leaf-green of a yellowish white. Still nearer to the middle, red and green are also differentiated and recognized as such. We may say, therefore, that the middle zone of our retina is green-blind, and explain that according to the Young-Helmholtz theory by the assumption that in this zone the red- and green-sensitive substances have become alike and equal to the former. Here red and green appear more or less yellowish, as both colors excite the R' and G' cells equally in the same way as dark or light yellow would. The outmost zone is totally color-blind, because here all the terminals contain the same photo-chemical substance.

We may refer here to the speculation of Donders, who considered that he could trace in the retina vestiges of several evolutionary steps, somewhat as follows:

1. Sensations of light and shade only.
2. Dichromic imperfect vision like red-blindness, with short spectrum and low sensitiveness to the long-waved rays.
3. Dichromic perfect vision like green-blindness, with full length of spectrum.
4. Imperfect normal vision, with low sensitiveness to certain colors.
5. Perfect normal vision.[1]

Apparently against this statement are the observations of Landolt,[2] who found that colored papers (about one square centimetre in size), if illuminated by direct sunlight, and, further, the spectral colors, if intense enough, are recognized in their color up to the extreme limits of our visual field; but Dobrowolsky and other observers after him objected that the color-perception in Landolt's experiment is due to diffracted light, which, falling on more central parts of the retina, is here recognized. It seems, therefore, fully justifiable to assume such an extreme achromatic zone with Helmholtz, Donders, Ole Bull, Preyer, Woinow, and other careful observers. At the same time it must be admitted that by practice our peripheral color-vision can be somewhat improved by a better education of the cor-

[1] Dr. Pole, loc. cit., p. 468.

[2] Annales d'Oculistique, Jan., Févr., 1874.

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responding brain parts. The extent of the peripheral field for white and colors is given in the following table:

	White.	Blue.	Red.	Green.
Externally	90°	80°	65°	50°
Out and up	60°	55°	45°	40°
Upward	45°	40°	35°	30°
Up and in	50°	45°	30°	25°
Internally	60°	55°	50°	40°
In and down	60°	50°	35°	30°
Downward	70°	60°	45°	35°
Down and out	85°	75°	55°	45°

We must not expect to find the same numbers for all normal eyes, especially as the pigments used in these examinations are by no means always the same. Here must be remembered what Landolt[1] says, that "no experience about the perception of colors is complete that does not take into consideration (1) the degree of the general illumination, (2) the brightness, and (3) the area of the color employed." That our peripheral color-vision depends also on the area of the colored object was first quantitatively shown by Aubert,[2] who at the same time demonstrated the influence of the background upon which the colored object is shown. According to him, the color of colored squares at twenty centimetres from the eye disappears at the following angles of deviation from the visual line:

Side of the Square in Millimetres.	Red.				Blue.				Yellow.				Green.			
	1	2	4	8	1	2	4	8	1	2	4	8	1	2	4	8
White background	16°	19°	26°	37°	15°	22°	36°	49°	21°	31°	44°		20°	36°	44°	50°
Black background	30°	32°	42°	53°	36°	48°	54°	72°	30°	32°	49°	47°	24°	27°	35°	45°
Average	23°	26°	34°	45°	26°	35°	45°	61°	26°	32°	42°		22°	32°	40°	47°

Aubert also found that a blue square of one millimetre side on a white background appeared black at ten feet distance, and so did a red one at twenty feet distance. A yellow and a green one fused completely with the white ground at twelve feet distance. On a black background, however, the green or the yellow square millimetre appeared as a gray point at sixteen feet, the red at twelve feet. Blue appeared blue when it was seen at all. Oliver[3] states lately that in order to be recognized on a black background and under diffused daylight at a distance of five metres it requires squares of the following sides for the different colors: two and two-thirds millimetres for red, a little more for yellow, eight and three-fourths millimetres for blue, ten and three-fourths millimetres for green, and twenty-two and three-fourths millimetres for violet.

[1] Loc. cit., p. 3.

[2] Graefe's Arch. f. Ophth., Bd. iii. p. 2.

[3] Text-Book of Ophthalmology, 1893.

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Here, again, attention must be called to the fact that the pigment colors are by no means always the same, so that for scientific experiments these pigments must be analyzed in the same manner as has been done by Captain Abney in the following table:

Colored Papers.	Wave-Length of Dominant Ray.	Percentage of White Light.	Percentage of Luminosity if White Paper equals 100.
Vermilion	610 $\mu\mu$	2.5	14.8
Emerald green	522 $\mu\mu$	59	22.7
French ultramarine blue	472 $\mu\mu$	61	4.4
Brown paper	594 $\mu\mu$	50	25
Brown paper	587 $\mu\mu$	67	19.5
Orange	591.5 $\mu\mu$	4	62.2
Chrome yellow	583.5 $\mu\mu$	26	77.7
Blue-green	500.5 $\mu\mu$	42.5	14.8
Eosine dye	640 $\mu\mu$	72	44.7
Cobalt	482 $\mu\mu$	55.5	14.5

This would mean for vermilion that this pigment being taken as 100, it can be exactly reproduced by mixing 97.5 parts of a spectral color of the wave-length 610 $\mu\mu$ with 2.5 parts of white light. Cattell[1] has shown that when the light reflected from colored pigments impinges upon the retina for too short a time, gray alone is seen, and that the time required for recognizing the color of a surface one by three centimetres on a white background with daylight from a clear sky varies between 0.0006 and 0.0027 of a second. The retina in these experiments was most sensitive to orange and yellow, requiring about 0.0009 second for their recognition, while it required 0.00121 second for blue, 0.00128 second for red, 0.00142 second for green, and 0.00232 second for violet. As pigments reflect light not only of one color, but usually of two or more colors, these results cannot be used to draw exact conclusions from for the relative inertia of the three photo-chemical substances, but they certainly show us that time is required to perceive the colors, and different times for different colors.

König, a normal trichromatic, and Brodhun, a dichromatic, have both made very careful experiments as to the minimum intensity of light that must exist to enable us to recognize the existence of an objective illumination in comparison with the perfectly dark background of the objective field. They found that this minimum amount of light—this "untere Reizschwelle," as Helmholtz calls it—is quite different for differently colored lights, and that it is least for blue. One might expect that the eye would observe the smallest amount of light; but, apart from the fact already mentioned,—the inertia of the retina,—there is another factor here that must be considered now as having a bearing on many phenomena mentioned in our article. The visual field of even a healthy man is at no time entirely free from a dim light, in which often changing spots of, it may be, fan-

[1] The Inertia of the Eye and Brain. Brain, vol. viii. p. 301.

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tastic appearance arise. This subjective light, that changes with every movement of the eye and lids and every act of accommodation, has been called by Helmholtz the *intrinsic light of the retina.* We recognize its presence only by the slight fluctuations of its intensity, the so-called *light dust* or *light chaos,* whilst the intensity itself, as calculated by Helmholtz according to the modified Fechner's law, is by no means so slight. This helps us to understand why the incoming light can be observed only after it has reached a certain intensity,—namely, that of the intrinsic light of the retina.

Lately, König and Brodhun[1] have made very careful and extended experiments about the smallest observable difference in differently colored lights. They have found that if one selects a suitable unity of illumination for the different spectral colors, the curve which represents the dependence of the smallest observable differences from the absolute light intensities shows for greater intensities only small, uncertain differences. In a weaker illumination, however, there is a considerable difference between the more refrangible and the less refrangible colors. In the first named, the blue colors, one can then observe much smaller differences of the objective light intensity than in the red-yellow colors. These observations are the more important as they form the basis for Helmholtz's new inquiry into the three primary color-sensations referred to above.[2]

So far we have spoken of color only as a momentary sensation, without regard to the subsequent changes that may be produced by its after-effect; for all light, of course, affects our retina not only at one moment, but for a considerable time after its objective disappearance, the simplest proof of which lies in the fact of our seeing a light, if quickly moved in a circle, not as a multitude of different lights, but as a circle of light, because the retinal impression of the light on one point of its circular path still remains, while at the same time in another and then in another it makes new impressions on our retina. It belongs to another paper in this System of Ophthalmology to describe these phenomena in detail. We only remind the reader here that these after-effects of light give rise to after-images, which are called *positive* when at the closure of the eye the light parts of the after-image correspond to the light parts of the object, and *negative* when each light part of the object appears dark in the after-image. If the light has affected the eye only a short time, and the visual field is kept free from all traces of external light, we see usually a positive after-image, which disappears gradually without becoming negative. This latter appears at once if, while the positive after-image still exists, one turns the eye to an equally illuminated surface. The color of the object and of the positive after-image is called the *primary* one, whilst that of the field later affecting the eye and producing the negative after-image is called the *reacting* light, because it shows the

[1] Sitzungsber. der Akad. der Wissensch. zu Berlin, July 26, 1888.

[2] Helmholtz, loc. cit., pp. 405 and 448.

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reaction of the retina. By the study of these after-images it has been shown (1) that after disappearance of the primary light the state of stimulation in the retina and visual apparatus lasts for some time, whence positive after-images result; and (2) that the same nervous substance affected before now perceives new light much less than do the parts of the retina not stimulated before, so that if new light falls into the eye the formerly stimulated area appears relatively dark as compared with the other visual field, thus producing negative after-images. If now we have looked at a colored object, and regard the after-image on a quite dark ground or a bright ground of different brightness, then, according to circumstances, a positive or a negative after-image will appear. The positive after-image is first, in the phases of its greatest luminosity, of the same color as the object, whilst the negative image, at least as soon as it is fully developed, shows a color complementary to that of the object. Thus, the negative after-image of red is blue-green; of yellow, blue; of green, rose red; and *vice versa*. This may serve as a good argument in favor of the Young-Helmholtz theory; for, as the colored light does not stimulate the three kinds of cones or photo-chemical substances equally, there must also follow an unequal degree of fatigue. If the eye has looked at red, the red-sensitive cones are strongly stimulated and fatigued, but the green and blue ones, to only a very moderate degree. If, now, white light falls into the eye, the green- and blue-sensitive cones of the formerly stimulated area will be more strongly affected than the red ones. There must, therefore, appear a color-sensation in which red is weak, but green and blue are dominant. In short, the after-image must appear blue-green. Corresponding results are obtained if one regards negative after-images of colored objects or colored grounds. From the color of the ground principally those constituents disappear which are most prominent in the primary color. Thus, a green after-image will appear red-yellow on a yellow ground, because the yellow of the ground (arousing as it does the red and the green sensations) excites the tired green fibres much less.

Of special interest are those cases in which the primary color of the object is complementary to the reacting one of the ground. If, for example, a blue-green piece of paper is placed on a red ground, and, after having been fixed steadily for a while, is taken away, there appears a beautiful saturated red after-image of the blue-green object, more saturated than if a black object on the same red ground had been looked at. The same observations have been made and verified by Helmholtz with pure spectral colors, whence he has drawn the important conclusion that the most saturated objective colors existing—the pure spectral colors—do not produce in the untired eye the most saturated color-sensations which are possible for us, but that we obtain these only when, before looking, we have tired our eye to the complementary colors. This seems to prove that even the spectral colors are by no means quite saturated. They contain, as the Young-Helmholtz theory especially calls attention to, a great deal of white from the simulta-

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neous stimulation of all the photo-chemical substances. Thus, it is evident that if the blue and green elements have been much fatigued, as in the previous experiment, they take almost no part in the production of the following sensation, so that the following red stimulates only the red-sensitive fibres, and appears, therefore, in a beautiful saturation.

Not only colored but also white objects give rise to colored after-images; but the complete description of this phenomenon cannot be given here, for want of space. We can only mention that thereby the differences in the remaining after-stimulation and the following fatigue for the different colors have been carefully studied by Helmholtz and others, and that the results are valuable for the explanation of the appearance of the whole spectrum in gradually reduced light, as before stated. The reader must be referred to larger books, such as Helmholtz's "Physiologische Optik," for a study of this subject.

Having described how succeeding colors influence each other mutually, we must now see how colors affect each other if at the same time in the visual field. These phenomena of subjective colors are usually described under the name of *contrast*, and especially *simultaneous contrast*, whilst those before mentioned fall under the head of *successive contrast*. This successive contrast plays, however, an important part also in many instances of apparently simultaneous contrast, when one compares colors which are beside each other in the visual field; for it is a fact that in the common use of our eyes we let the point of fixation unconsciously wander in the field, so that it glides successively over the different parts of the object looked at. When, therefore, the eye slowly wanders over an object, an after-image is produced, which, however, as being only an indistinct spot, is usually not recognized, though an attentive observer will see it. If now the eye look at a neighboring field of another color, of course this color must be changed by the influence of the after-image of the first one. If we place, for instance, upon a sheet of colored paper a small circle of white or gray paper, this will appear in the complementary color. The same principle helps us to understand how the effect of contrast is the greater the nearer the two colors are to each other, because the eye under those circumstances has not time to recover as quickly as it could if the two colors were far apart. We cannot give more examples here, but the results of all the experiments, as Church[1] remarks, confirm in every particular the Young-Helmholtz theory.

With regard to the phenomena of pure simultaneous contrast, however, we cannot make use of the wandering of the eye, because they appear even if the eye is held as steady as possible. Helmholtz regards them as due to deceptions of judgment, because we are inclined to look upon those differences which are distinctly to be observed in the perception as greater than those that are seen only indistinctly in the perception or that have to

[1] Color, by Professor A. H. Church, 1887, p. 102.

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be judged by the help of memory. A colored field, if looked at steadily, will soon begin to appear gray, and a small square of gray on a surface of green, when covered with a transparent sheet of tissue-paper, appears in a distinct rose red. Helmholtz says, "When in the visual field a special color preponderates, this gradually appears in a whitish shade, while real white then appears in a complementary color. Our mind changes the standard of what we call white." The best example of simultaneous contrast is seen in the colored shadows, especially if the colors are not too saturated. If, for example, a sheet of white paper is illuminated at the same time by daylight and by candle-light, and a pencil is placed on the paper, two shadows will appear. One is thrown by the daylight, but, being illuminated by the red-yellow light of the candle, appears red-yellow. The other is thrown by the candle and illuminated by the white daylight. It appears *blue*, complementary to the color of the other shadow. That this blue is produced by an error of judgment the following experiment seems to show. If one looks through a blackened tube on a spot that belongs partly to the white ground, partly to the shadow produced by the candle-light, the second part appears blue. If the tube is now moved so that nothing is seen but the shadow of the candle-light, the whole visual field appears blue, and remains so even if the candle is removed entirely. The blue disappears only if now the tube is taken from the eye. This explanation of these phenomena of pure simultaneous contrast by errors of judgment has often been objected to, and indeed it seems to be insufficient, though the psychical factor cannot be denied. It is this class of subjective colors that has given such prominence to a new theory of color-perception, that of Hering. A long time before Hering, Plateau had attempted to explain these colors on the assumption that the light on one part of the retina produced an indirect effect on the adjacent parts, a kind of antagonistic activity of the retina that gave rise to the complementary colors. But though on such a theory it is difficult to explain how the gray circle on the green paper appears in a more distinct rose red when the green color is made more indistinct by the tissue-paper, still nothing hinders us from assuming such a spreading activity also among the Young-Helmholtz color-sensitive terminals in the retina, if decisive experiments oblige us to take such a stand. That would in no way affect the Young-Helmholtz theory, but would only oblige us to accept Plateau's principle.

Lately, Alfred M. Mayer[1] has studied these phenomena of pure simultaneous contrast anew very carefully, and has estimated the interval between an electric flash that probably lasted less than one-millionth of a second and the perception of the complementary contrast-colors as less than one-fifteenth of a second. Mayer considers this time as too short for errors of judgment; but this is certainly not correct, as there are many instances

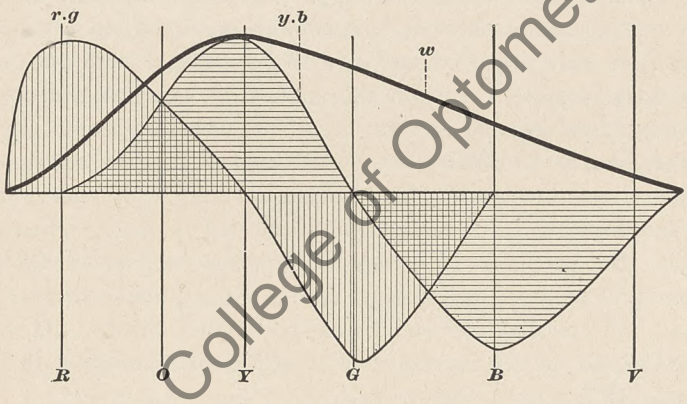
[1] American Journal of Science, vol. xlvi., July, 1893.

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which show that we make such false judgments instantaneously, as, for instance, Zöllner's line[1] will demonstrate easily.

And now we have to describe in a few words Hering's theory of color-perception, which in the last twenty years has sprung up as a rival theory to that of Helmholtz. This theory, as Helmholtz remarks,[2] is a modification of Young's. It assumes the existence in the retina of three visual substances,—a whitish-black, a red-green, and a yellow-blue substance. In each pair the one color is complementary to the other, so that the red must be more of a purple. The theory further assumes that the different colors affect the different substances differently. Red light, for example, induces a katabolic change (Dissimilirung) in the red-green substance, giving rise to a sensation of red; while green light gives rise to constructive or anabolic changes (Assimilirung) in the same substance, thereby producing the sensation of green. In the same way katabolic changes in the yellow-blue substance induced by yellow rays of light give rise to the sensation of yellow, while anabolic changes in the same substance are induced by blue, giving the sensation of blue. The white-black substance, however, is affected in a katabolic way by all the colors of the spectrum, though in a different degree, producing in us the sensation of white, whilst its anabolism gives the sensation of darkness. If now red and green light together strike the retina, the anabolic and katabolic changes are in equilibrium in the red-green substance, and no color-sensation is produced, except that which results from the simultaneous action of both colors on the white-

FIG. 4.



black substance, by which we see white. The accompanying diagram, from Foster's "Text-Book of Physiology" (sixth edition, part iv. p. 95), may serve to illustrate this view better.

The lines *R*, *O*, *Y*, *G*, *B*, *V* indicate the position on the spectrum of red, orange, yellow, green, blue, and violet. The line *r.g*, which includes a

[1] Text-Book of Human Physiology, by Landois and Stirling, third American edition, p. 843.

[2] Loc. cit. p. 376.

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space shaded vertically, is intended to represent the effect of rays of different wave-lengths on the red-green visual substance. In the red, orange, and yellow, up to the line *Y*, the effect is katabolic, one of dissimilation (red sensation). *Y* marks the position of equilibrium; beyond this the effect is anabolic, one of assimilation (green sensation). The line *y.b* similarly represents the behavior of the yellow-blue substance shaded horizontally, katabolic (yellow) up to *G* and anabolic (blue) beyond. The line *w* indicates the white-black substance, unshaded, katabolic (sensation of white) along the whole length of the spectrum.

The main feature of this theory consists in establishing an antagonism between red and green and between yellow and blue, by connecting each sensation with opposite states in the metabolism. On page 595 attention has been called to this point, and there the antagonism of this theory to the best-established facts of our nerve-physiology has been pointed out. This last objection is also admitted by Professor Ebbinghaus in his latest contribution to this subject, mentioned before. He still clings to the three visual substances, but he allows only katabolic changes in each to produce the corresponding sensations of white, red, green, yellow, and blue, although by this means he loses the plausible explanation of an antagonistic relation between the two colors in each pair, and it is difficult, if not impossible, to understand him when he says (page 236, *op. cit.*), "Blue and yellow are antagonistic colors. If the stimulation of each stands in a certain quantitative ratio, the chromatic character of the sensation is abolished." For Ebbinghaus the yellow-blue substance is identical with the visual purple, which he supposes to exist not only in the rods but even in the cones, where it has never been found, an absence which he explains as only apparent and due to its mixture with the red-green substance that is present only in the cones and, being complementary in color to the other color-substance, makes the cones appear colorless. It seems, therefore, as if Ebbinghaus, providing as he does each cone with the red-green and the yellow-blue substance, makes the nerve transmit different impulses according as the cone is affected by red, green, yellow, or blue light. But, as observed before, this appears very questionable in the face of our present nerve-physiology, so that Ebbinghaus's theory does not seem to be able to displace the Young-Helmholtz theory. It, however, weakens Hering's theory the more, as it again calls attention to the vital physiological difficulty of that view.[1]

Color-blindness, by Hering's theory as well as by Ebbinghaus's modification of it, is produced by the absence of the red-green visual substance, giving *red-green* blindness, or by the rare absence of the yellow-blue substance, giving rise to *yellow-blue* blindness, or by the combined absence of

[1] The reader will find a very able discussion of Ebbinghaus's theory of color-vision in Mind, New Series, No. 9, January, 1894, by Chr. L. Franklin, who shows that the visual purple cannot be employed for the explanation of color-perception in the manner assumed by Ebbinghaus.

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the red-green and yellow-blue substances, producing *total color-blindness.* The difference between red-blindness and green-blindness Hering attributes to a different coloration of the media of the eye, partly of the macula lutea and partly of the crystalline lens. The latter, however, occurs only in diseased or very old eyes, whilst the coloring-matter of the yellow spot shows its undeniable effect mostly on greenish-blue rays, and hardly any on those rays that would establish the difference above referred to.[1]

Of course it does not lie within the scope of this paper to give anything like an exhaustive critical consideration of Hering's theory. However in the future the intellectual fight may be decided, whether in favor of Helmholtz or of Hering or of some new theory, at present the modified Young-Helmholtz theory seems to explain best all the phenomena, and it has therefore been accepted as the clue through the labyrinth of the complex facts of color-perception.

A few words may be added about the development of our own color-sense. Although the efforts to prove that on account of their limited vocabulary for colors the ancients had an imperfect appreciation of colors have been shown to rest on invalid grounds, still there can hardly be any doubt that our color-sense was gradually developed, and the question may be asked, How did these three primary sensations of color arise? The first perception was very likely that of simple light and darkness, which is all we possess even now at the most peripheral parts of the retina. Later the retina became better differentiated to distinguish between those lights that were of most interest to the life of our prehistoric ancestors and those that were most powerful to affect the eye. It seems that blue must be regarded as the most primitive sensation of color, for "the first sensation of light is what answers to the blue sensation when it is strong enough to give the sensation of color." As Captain Abney says,[2] "It appears probable that even in insect life this violet (blue) sensation is predominant, but at all events existent. Insects whose food is to be found on flowers seek it in the gloaming, when they are comparatively safe from attack. Professor Huxley states that the greatest number of wild flowers are certainly not red, but more or less of a blue color. This means that the insect eye has to distinguish these flowers at dusk from the surrounding leaves, which are then of a dismal gray; a blue flower would be visible to us, while a red flower would be as black as night. That the insects single out these flowers seems to show that they participate in the same order of visual sensations." Blue is the color of the heavens, where at a much later period man placed his gods. As such, long before that time, this blue entered his eye continually in his out-of-doors life when the sky was not clouded, and even now it is recognized farthest toward the periphery of our retina.

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[1] Helmholtz, loc. cit. p. 383.

[2] The Sensitiveness of the Eye to Light and Color. Lecture delivered at the Royal Institution of Great Britain.

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Next to blue, probably yellow became first developed in man's visual sensation, so that all lights of long wave-lengths (red, yellow, green) appeared yellow, while those of short waves appeared blue, as is still the case in certain peripheral parts of the retina. Later the yellow sensation became differentiated into a green and a red one, when the green of the vegetation made its deep impression upon his eye and mind, which color, according to the latest investigations of Helmholtz, seems to correspond best to our green sensation. At the same time red followed, impressing him most deeply from the beauty of the rising and of the setting sun, and, above all, "from the embers of the hearth-fire," which must have played so important a part in prehistoric times. To this, as remarked by Gould,[1]—who advocates, however, four primary sensations,—we must add "the *rôle* that war and blood-shed, blood-sacrament and blood-rites, have acted in the history of the race from man's egress out of animalism and progress to nineteenth-century militarism." Perhaps thus we may explain how from the mere light-perception our three primary color-sensations have arisen, by means of which we are now enabled to enjoy the marvellousness of our whole color-universe.

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[1] The Meaning and Method of Life, by G. M. Gould, M.D., 1893.

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PHOTO-CHEMISTRY OF THE RETINA.

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TRANSLATED BY

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THE "adequate" irritations which impinge upon the peripheral terminal apparatus of our organs of special sense vary so much in quality and quantity from those which the conducting paths of this apparatus (the nerve-fibres) are able to excite, that they must first be transformed into nervous irritations in the terminal organs in order to attain the central organ along these paths. Nervous irritations are of a mechanical, chemical, thermic, or electrical nature, and into such irritations must external ones be transformed when they vary in quantity, or when they are of a different quality, such, *e.g.*, as waves of sound or of light. For example, the chemical processes which are capable of exciting the olfactory mucous membrane must be altered, at least in quantity.

The first observation of such a transformation, objectively visible, was made by Hensen,[1] who recognized that the aerial vibrations of sound cause vibration of the fine hairs in the ears of the mysis in the same way as a mechanical irritation could produce it. In the other higher organ of sense, the eye, Holmgren[2] first demonstrated the transformation of light into electrical processes, whilst later it has been shown in the same organ that not only electrical but other phenomena take part in this alteration. Subsequently Boll made the far-reaching discovery[3] that the retina of most animals appears of a purplish red, and that during life this color disappears under the influence of light. It was reserved for Kuehne,[4] however, first to prove that this process is really chemical.

Finally, even mechanical alterations due to the action of light have been recognized in the eye; for example, those first seen by Boll[5] in the retinal

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[1] Zeitsch. f. vergleich. Zoologie, xiii. S. 319.
[2] Upsala Fort und Lingar, Band i., January, 1866, Ss. 184–198.
[3] Monatsber. d. Berliner Akademie, November 12, 1876.
[4] Verhand. d. Naturhist. Med. Vereins zu Heidelberg, January 5, 1877.
[5] Monatsber. d. Berliner Akademie, February 15, 1877.

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epithelium, and later correctly explained by Kuehne.[1] Moreover, the alterations in the form of the cones in the illuminated and non-illuminated retina have been observed and explained conjointly by Engelmann and Van Genderen Stort. Whether all these processes have their direct primal cause in light itself, or are of a secondary nature, is not known, but it is positive that they are so intimately connected with one another that those which are not chemical must be considered in this chapter. Moreover, our knowledge of these chemical processes demands that we should make a thorough study of the chemical structure of the retina, and this we shall now lay out in detail, so far as it is known to date, though acknowledging that the results of such a study are still far from perfection.

THE RETINA AS A WHOLE.

The extreme instability of the retina is shown by its rapid disintegration after death. It yields with extraordinary lack of resistance to decay; but even before it falls a victim to bacteria it exhibits many striking alterations. In life it is smooth and transparent; in death it becomes wrinkled and opaque. The opacification begins in the anterior layers; dissolution of the external layer, of the rods and cones, as described by Max Schultze, into columns of delicate rods next appears; later the internal and external membranes separate from one another, and the latter curves over into the shape of a shepherd's crook, or even curls into complete circular coils. The satiny sheen described by Boll,[2] after the disappearance of the purple tint, as the second stage of the alteration, is not, in Kuehne's opinion, due to death, because this condition can be produced by pressure, and can occasionally be made to disappear. This phenomenon must be regarded as simply due to a slanting and a dislocation of the rods. Inasmuch as the destruction of tissues in general is closely connected with the cessation of the circulation of the blood, it is remarkable to find so few blood-vessels in the retina. In the inner layer there is nothing but a capillary net-work, which does not pass farther forward than the external granular layer. The external half, therefore, of the epithelial layer of the retina is, like many peripheral glands, nourished by lymphatics, the material for which is chiefly furnished by the vessels of the choroid.

On account of the strongly alkaline reaction of the vitreous, it is not easy to establish the reaction of the retina. At Rollet's suggestion, Chodin made a series of careful studies to decide this question,[3] and found such a reaction to exist in fresh retinæ, as well as in transverse sections of the optic nerve, it being acid especially when, with the neatest possible removal of the vitreous, the retina, at first reacting alkaline, was crushed and

[1] In various articles which will be specified later in this paper.

[2] Zur Anatomie u. Physiol. d. Netzhaut, Monatsbericht d. Berliner Akademie, November 12, 1877.

[3] Ueber d. chem. Reaction d. Netzhaut und d. Sehnerven, Sitzungsber. d. Wiener Akad., January 19, 1877.

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exposed to light. The reaction in the retina of the frog is less constant, but is generally inclined to be acid. The retinæ of animals kept in the dark for a long time previous to death seem to react with less acidity. Cöhn asserts[1] that fresh retinæ exhibit an acid reaction on the side of the rods and cones. He also says that if the retina is kept for a long time, and especially in the dark, the reaction rapidly becomes alkaline. Kuehne has always found[2] the retinæ of frogs remaining in the dark to be alkaline. He states that this is so even after careful removal of the vitreous and crushing under light. Therefore, since Gscheidlen[3] has always found the gray substance of the brain and spinal cord to be acid, and Chodin the white substance in dogs' brains the same, though less distinctly marked, Kuehne believes that the acid reaction of the retina must be referred to the conducting portion of the apparatus.

C. Schmidt has found albumin in the retina.[4] Kuehne attributes the opacification of the retina after death, which appears in frogs that are placed at a temperature of 45° C. (112° F.), to a substance resembling myosin. Cohn insists on the presence of muscular and serous albumin. C. Schmidt has discovered a peculiar substance which does not coincide with glutin, mucin, or so-called chondrin. Cohn has found genuine mucin, but has not determined the presence of any glutin. C. Schmidt has discovered a body which crystallizes with platinum chloride and smells strongly of trimethylamin, the latter originating from cholin as a product of the decomposition of lecithin.

In ultra-violet light the gray substance of the retina shows a pale whitish-blue and slightly changeable fluorescence.[5]

THE RETINAL EPITHELIUM.

The cells composing the retinal epithelium consist of a summit, a base, and a process.

The base is to be regarded as a disk, which is perforated with cylindrical channels for the reception of the external members of the retina, the rods. The processes vary in form, and may extend as far as the external limiting membrane. Schwalbe has described[6] a system of cementing lines or beams which exist between the cells, but says that they are actually optical sections of a firmer portion of the cells that are composed of neurokeratin, which, owing to the manner in which it rests upon the cells, has been called *the hat*. Kuhnt[7] has found it extending almost to the basis of

[1] Zeitsch. f. Physiol. Chemie, Band v. S. 213.

[2] Untersuchungen aus dem Physiologischen Institut der Universität Heidelberg (for the sake of brevity, hereafter H. U.), i. S. 22.

[3] Arch. f. d. Ges. Physiologie, viii. S. 171.

[4] Communicated by Blessig. De Retinæ, Inaug. Diss., Dorpat, 1855.

[5] Ewald and Kuehne, H. U., i. S. 317.

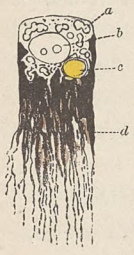
[6] Handbuch, i. S. 224.

[7] Monatsbl. f. Augenheilk., xv. Jahrgang, S. 72.

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the cells, where, when near the margin, according to Angelucci,[1] it coalesces with the hats of the adjoining cells. The summits of the cells have a slightly striated protoplasm, while a majority of them have a bright, ellipsoidal, transverse nucleus. The soft protoplasm, which swells a little in acids, gradually breaks down in a ten per cent. solution of salt, and dissolves with the greatest ease in a solution of biliary acid and in alkalies that vary from one to five per cent. The brown pigment consists mostly of globules and granules, and extends slightly upward at the margin of the summit. A short time after death it retracts somewhat at the margin, so that the borders of the cells appear broader.

FIG. 1.



Cell of the retinal epithelium of the frog.—*a*, myeloidin granules; *b*, nucleus; *c*, drop of fat, globule of fat; *d*, pigment process. (Kuehne.)

In many animals the summit contains a remarkable amount of fat. In the frog, in a few owls, and in rabbits, especially those that are albinotic, fat is always present. It has not yet been discovered in man, cattle, or swine. It generally appears in the form of a single drop which is as large as the nucleus of the cell. If there are several drops, a number of small ones group themselves around the larger ones. Occasionally segmentation of some of the smaller drops, or a change in its form, or an arrangement in layers on its surface, may be seen. The fat is almost always found in the anterior portion of the summit, near the nucleus. In frogs it varies from a deep golden yellow to a pale lemon. It is very brilliant where segmentation has occurred, this probably not resulting from the minuteness of the drops alone, but from their lack of pigment. A few species of owls are the only birds in which fat has been thus far discovered; in some it is colorless, in others it extends from yellowish to orange. The finely granular, zigzag, deeply tinted specimens are probably excreted pigment with a trace of fat. The gigantic drops of the rabbit's retina are but slightly pigmented. As this epithelial fat remains fluid at low temperatures, it probably consists chiefly of olein. It can be easily extracted by alcoholic ether, benzol, or sulphuretted carbon. Alkalies and bile do not affect it. Osmic acid quickly tints the globules a deep brown.

The yellow pigment of the fat-globules in frogs—the lipochrin—is exhibited thus.[2] The retinæ of a large number of frogs are placed in alcohol, which they tint very slightly. Ether is used to extract the pigment fat. This form of fat cannot be distinguished from that which is found in the folds of the abdominal cavity of frogs. It gives the same spectrum in ether and in sulphuretted carbon. When removed into a hot alcoholic solution with caustic soda, it yields a yellow soap from which ether, except for a slight contamination with soap, extracts the pigment almost pure. After evaporating the ether, the pigment is found to be amorphous. The spec-

[1] Arch. f. Anat. u. Physiol., Phys. Abth., 1878, S. 353.
[2] Kuehne and Ayres, H. U., i. S. 341.

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trum of the ethereal solution is identical with that of frog's fat, whilst that of the deep orange sulphuretted solution is slightly different. If the latter is evaporated and again absorbed by ether, the genuine ether spectrum can once more be produced.

In solutions of iodine and iodide of potassium and a trace of alcohol, lipochrin becomes greenish to bluish green; in nitric acid it becomes yellow-green; in concentrated sulphuric acid it becomes dark violet to brown. If it be kept in solutions and exposed to intense sunlight it bleaches in two or three hours. The color is not restored in darkness. In the dark it is bleached by ozone.

Although lipochrin exhibits some similar reactions, such as the blue color in death and the reactions with nitric and sulphuric acids, it is not the same as lutein.[1] It differs from lutein in its destructibility by light; it is never crystalline, and it gives a different spectrum.[2] The skin of frogs gives off a pigment to ether, especially after previous dilution, which bears some resemblance to lipochrin, this being occasionally mixed with another greenish or bluish pigment.

The summits of the epithelial cells contain, in addition to the fat, some colorless masses, shining like wax. These are oval, oblong, zigzag, semi-lunar, or cylindrical in shape. Boll probably saw them,[3] but erroneously regarded them as colorless fat. Ewald and Kuehne called them myeloidin granules, and differentiated them from fat. They are generally situated directly behind the nucleus, and are often so numerous that they fill the entire summit. They yield somewhat to ether, chloroform, and benzol, without swelling or entirely dissolving. Under osmic acid they slowly become a pale or dirty bluish green. They swell greatly in alcohol, like the myeloidin of the rods, and gradually decay. They are readily soluble in from one to five per cent. of bile. They have been discovered in frogs (not invariably, but when present always in some epithelial cells), in a few owls, and in the buzzard. Light has no influence upon their number.

The base and the processes of the retinal epithelium are filled with epithelial pigment. The pigment is absent in albinos. The cells in front of the tapetum are more or less scantily provided with pigment. In many animals (beasts of prey and fishes) the pigment is replaced by larger or smaller iridescent crystals. The pigment is always brown, even in thick sections. For that reason Kuehne calls it fuscin. It looks most like choroidal pigment. It is darkest in frogs, lighter in men and birds, from a chocolate to a cinnamon brown; in fishes traces of reddish or purple are seen;[4] in invertebrates a black pigment is found; and in the astacus[5] a fine, yellow, crystalline pigment can be recognized.

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[1] Capraniva, Arch. f. Anat. u. Physiol., Phys. Abth., 1877, S. 285.
[2] Kuehne and Ayres, loc. cit.
[3] Archiv f. Anat. u. Physiol., Phys. Abth., 1877, S. 1.
[4] R. Wagner, Lehrbuch d. Zoologie, 1843, S. 250.
[5] W. Szczawinska, Arch. di Biol. de Gend.

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Whilst choroidal pigment is granular, the fuscin of the retinal epithelial cells is mostly rod-shaped, suggesting a form of crystallization. Rosow[1] has attempted to fix this pigment by macerating retinæ in water up to putrefaction, but in this attempt the bacteria gave rise to a most disagreeable pollution.

Kuehne[2] exhibited small masses of fuscin by dissolving the retinal epithelium in five per cent. bile and washing it with water, alcohol, and ether. At Kuehne's suggestion, the writer has, by the aid of trypsin digestion,[3] been able to show larger masses of choroidal and retinal pigment combined. These were obtained from the eyes of hens. The eyes were placed in alcohol, extracted with ether, boiled with water, and then subjected to a whole day of trypsin digestion. The masses were filtered through gauze, washed with alkali to dissolve the nuclein, and the alkali in turn was washed out with water.

Fuscin is not easily affected by chemicals. Concentrated alkalies and acids absorb but little of it, even after prolonged boiling. Rosow asserts that it dissolves easily, with a violet tint, after treatment with nitric acid in alkalies, from which by neutralization it is again precipitated. The writer has verified this ready solubility after the nitric acid treatment, but the solutions were *yellow*, and from them he has failed to get a pigment precipitate by acids. Moreover, he has found that the solubility in alkalies depends on the amount of light and warmth, or even of light alone. Solutions made in this manner yielded on neutralization a precipitate of pigment in brown masses. As nitric acid produces oxidation, he tried other oxidizing materials, but found that ozone, *e.g.*, had no influence upon the solubility. If the solution is not acid, nothing is dissolved, even with warmth. It is remarkable that this substance, which acids can hardly touch, should be so sensitive to light, as discovered by Kuehne and later carefully investigated by himself. He has found that even desiccated fuscin shows more or less sensibility to light: it is slight in frogs and hens, moderate in owls, and most noticeable in fish (*Abramis brama*).[4] Moist fuscin grows paler in the presence of acids than when dry, this being particularly so in alkaline fluids. Fuscin discovered in these fluids is generally heavier than the pigment granules that are suspended in the same. The latter at last become colorless, but maintain their form, so that it becomes necessary to imagine a substratum that is first impregnated with the pigment. If oxygen is present, even the moist preparations fail to bleach. On the contrary, solutions grow paler in the dark when treated with ozone, whilst in the light the same agent rapidly bleaches them. Pure fuscin contains nitrogen and iron.[5]

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[1] Archiv f. Oph., ix. 3, S. 63.
[2] H. U., ii. 1, S. 112.
[3] H. U., iii. S. 324.
[4] Kuehne and Sewall, H. U., iii. 3 and 4, S. 237.
[5] Mays, Archiv f. Ophth., xxxix. 3, S. 89.

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THE VISUAL CELLS (RODS AND CONES).

Whenever the rods and cones appear together, the rods alone extend to the base of the epithelial cells. When the cones predominate, they, too, extend partly into the summit free of fuscin. In the retinæ of snakes, which have no rods, all the conal processes extend beyond the posterior fuscin zone. The same may occur in the fovea centralis of man and the ape.

The internal members have a transparent protoplasm. There are nuclear bodies which produce marked and excessive refraction of light. Particularly is this so with those ovoidal, moon-shaped, and parabolic bodies which occur in the lower vertebrates in the rods and in the higher vertebrates in the cones. Finally, the fibrous baskets that were discovered by Max Schultze are most developed in the cones of man. All these structures become slightly tinted by osmic acid, but grow dark much earlier and to a greater degree than the protoplasm. They seem partly related to fat and partly to myelin. Many reptiles and birds have actual pigmented fat globules. Moreover, the inner members of the cones in many birds and reptiles are interspersed with minute granules of rose-colored or yellowish pigment, which has probably been contaminated with fat.

The transition from the inner to the outer members is apparently a sudden one, yet, according to Dreser,[1] a process of the inner member seems to extend like a mesh-work into the interior of the outer member of the rods. The latter (cylinders) have a cylindrical or ellipsoidal section, are often hollow, and have irregular ends, looking as if they had been gnawed off. The cones have ninepin-shaped external members, with gently rounded tips. These external members are soft, pliant, and perishable. They are of weak refraction, and are easily separated from the inner members. The transverse striation of the tips is somewhat broader after death. Osmic acid tints the cylinders darker than the tips.

The cylinders swell in a half per cent. solution of salt[2] in the same way as Rumpf discovered that the axis-cylinders of the nerve-fibres do. They have a separable envelope, which reacts like neurokeratin[3] and has a resistance like that of the brain. Owing to this attribute, they may be regarded as cellulose. Neurokeratin, however, contains nitrogen and sulphur, and these remnants of rods do not show a cellulose reaction, but one of xanthoproteinic acid. Plates and interstitial tissue cannot be differentiated chemically.

The pigmentation by osmic acid, first observed in the rods by Max Schultze and Rudenew,[4] affects the myeloidin of the rods. Owing to its rapid appearance, it reminds one of that of the nerve medulla, but it is of another shade. With osmic acid, fat becomes yellowish brown or reddish brown, and

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[1] Zeitsch. f. Biol , xxii. S. 23.
[2] Dreser, loc. cit., Ss. 33, 34.
[3] Kuehne, loc. cit.
[4] Arch. f. Mic. Anat., i. S. 300.

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finally black; nerve medulla, bluish gray or bluish black; rod cylinders, greenish brown or greenish black, like that of the myeloidin of the epithelial cells, except that the latter are much brighter, as are the ends of many of the rods.

Dreser[1] believes that the myeloidin ought to be identified with vitellin. It is just as difficult to extract any solutions which will react the same to osmic acid after evaporation from myeloidin as from nerve medulla. Although alcohol-ether extracts everything from them which osmic acid stains, yet, like fat, they react brownish. The cylinders of frogs are rich in myeloidin. The tips, many rods in mammals, and the granules of the epithelium have but little myeloidin.

The ether in which retinæ have been treated in warmth deposits in small amounts, on cooling, a substance which is presumably lecithin. From warm alcohol a substance acting like cerebrin is obtained. In diluted alcohol the cylinders swell enormously and roll into clumps. Rapid freezing followed by thawing produces the same results. Most surprising of all is their behavior in one to five per cent. solutions of crystalline bile. Here the cylinders and tips of all the visual cells of all animals easily dissolve, leaving empty delicately walled sheaths. With fresh rods the solution is so sudden that they look like bursting rockets filled with coins. Since gall dissolves on the one hand albumin, and on the other lecithin, cerebrin, etc., it unites the properties of the aqueous and the alcoholic solutions.

PIGMENTS OF THE VISUAL CELLS.

Hannover[2] was the first to describe pigments in the oil globules of reptiles and birds. He found all the colors of the spectrum, and purple, in birds. Many reptiles have yellow oil globules. Max Schultze[3] has described red ones in the turtle. Carmine-red pigment had long been recognized in the eyes of many invertebrates, but it was first noted by Krohn,[4] in 1839, as the beautiful rose color of the rods of cephalopods. Leydig found rose and violet pigments in insects; Max Schultze found the same in crabs. H. Mueller[5] first saw a few red rods in the frog. Leydig again[6] investigated this point in amphibia, and saw with the naked eye a brilliant sheen in the fresh retina of the frog. He described the color as rose red, as Schultze had done.[7] He also saw it in the rods of the rat and the duck. These observations remained unnoticed till Boll[8] turned universal attention to the extensive and constant occurrence of pigmented rods. He also dis-

[1] Loc. cit.
[2] Arch. f. Anat. u. Phys., 1842, S. 320.
[3] Article "Retina" in Stricker's Handbuch d. Mic. Anat.
[4] Verhand. d. Leopold. Carolin. Akad., xix. 2, S. 45.
[5] Zeitsch. f. Wiss. Zool., iii. S. 234, and viii. S. 71.
[6] Lehrb. d. Histologie, 1857, S. 238.
[7] Archiv f. Mic. Anat., ii. 199 and 208.
[8] Monatsb. d. Berliner Akad., November 12, 1877, and Accad. di Lincei, December 3, 1877.

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covered green rods in the retina of the frog. He further found that frogs kept in the light had paler retinæ, and that if they were held in the sunlight their retinæ appeared bleached. He asserted that the color in the enucleated retina of a frog persisted scarcely for a minute, and in the eye of mammals but a few seconds, after death. He found that frogs exposed to direct sunlight had the retinal color restored almost instantaneously after the animal was removed to a darkened room. Boll suggested that the eye should be halved quickly, the retina removed without pressure (which destroys the color), and examination made with the naked eye or the microscope. He believed that in mammals the conditions should be examined with the ophthalmoscope. He ascribed the "proper color," the "purple color," to the stratified substance of the rods and cones of all animals (except the cones of reptiles), but he failed to express any opinion as to whether this tint depended upon a pigment or upon the phenomena of interference.

Whilst Boll regarded the disappearance of the pigment after death as a post-mortem condition, Kuehne found that the retina in a weak light (from a small hole in a shutter covered with a yellow cloth) preserved its color for hours. He also determined that in daylight the tint was lost at once. This test succeeded with disintegrated, crushed, and minced retinæ, as well as with those that had been treated with ammonia or had been hardened in alum. In this way it was decided that the bleaching is not due to death, but to the action of light, and that the color is not due to structural relations, but to a pigment (the visual purple) which is decomposed by light; thus proving that the whole resulted in a rapid photo-chemical disintegration of the retina.

THE VISUAL PURPLE (RHODOPSIN).

The visual purple[1] can be seen by the naked eye or the microscope, under the light of a sodium flame, in the fresh retinæ of animals which have been kept for an hour or two in the dark or in a moderate light. (Fig. 2.) In frogs, the optic nerve can be snipped with scissors and the eye halved equatorially. In mammals, the papilla in the halved eye is struck out on a lead plate with a punch, in a half per cent. solution of salt. In birds, the fundus is prepared by two cuts with scissors running nearly parallel to the pecten and meeting at its central terminus. Human eyes kept on ice for a day can still be used. If the retina sticks to the epithelium, as in apes, the eye should be left for a day in a four per cent. solution of potassic alum.

Visual purple occurs in almost all vertebrates, but only in the rods. The exceptions are one bat (*Rhinolophus hipposideros*), the hen, and the pigeon, although Van Genderen Stort[2] asserts that he has discovered it in one pigeon (*Columba Livia*), whilst Boll has seen traces of it in all pigeons. It has been recognized in man by Fuchs and Walponer,[3] and by Schenk

[1] Compare Fig. 5.

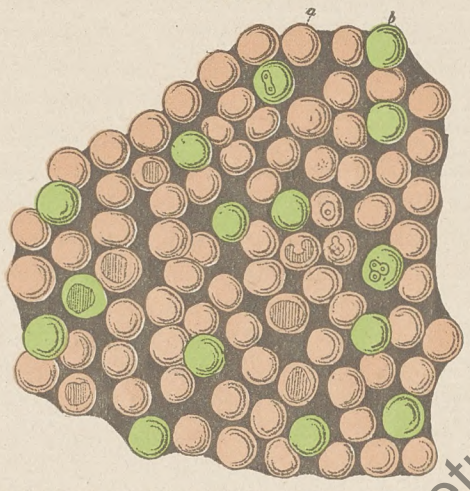
[2] Archives Néderlandoises, xxi. p. 40. (Reprint.)

[3] Wiener Med. Wochensch., 1877, S. 221.

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and Zuckerkandl.[1] In late years Kuehne and Nettleship[2] have often seen it. Michel and Rosenthal, on the contrary, never could find any traces of it.[3] Animals living in the dark possess it, and it has been discovered in embryos.[4] The anterior portion of the retina over a zone of three or four millimetres wide in man, apes, and other animals is free from visual purple. The rods of the macula lutea in man do not seem to possess it. Rabbits, oxen, sheep, and full-grown dogs and cats exhibit it in horizontal line as a more darkly tinted stripe. In rabbits it is distinctly elevated,—*the visual ridge.* In other animals it is flatter,—*the visual girdle.* Owls,

FIG. 2.



Microscopic view of the frog's retina from behind.—*a*, purple rods; *b*, green rods. (Kuehne.)

most fishes, man, and sheep have a purple shading to violet, which may be regarded as a mixture of visual red with visual violet or blue. This, however, is not so: it is a different substance chemically, as Kuehne and Sewall have shown in the fish.[5]

In order to exhibit the visual purple, solutions of from one to five per cent. of crystalline bile, free from ether and alcohol, should be used. The work should be done in a dark room that is lighted with sodium flame. The retinæ must be fresh, especially when taken from warm-blooded animals. According to Ayres,[6] they are longer utilizable if placed in a ten per cent. salt solution, as this probably retards coagulation of the myosin bodies. The filtrate is best filled with rock salt, which carries off the suspended fuscin and albuminous corpuscles. A clear, beautiful purple solution,

[1] Allgem. Wien. Med. Zeit., May 13, 1877.

[2] Journal of Physiology, ii. p. 38.

[3] Centralb. f. d. Med. Wiss., 1877, No. 24.

[4] Fuchs and Walponer, loc. cit.; Kuehne, Hermann's Handbuch d. Physiol., iii. S. 236; Albertini, Centralb. f. d. Med. Wiss., 1880, No. 40.

[5] H. U., iii. 3 and 4, S. 269.

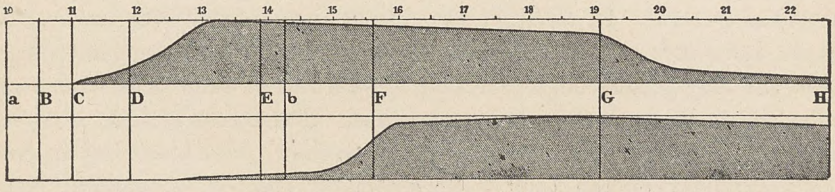
[6] H. U., ii. 4, S. 444.

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which in daylight turns red, yellow, and finally becomes colorless, is thus obtained. If diluted with water it becomes rose-colored; if it is more strongly diluted it turns lilac: tints which never arise from a pure red. If these solutions are dialyzed the membrane contains a deep purple myelin-like magma which is as sensitive to light as the retina.[1] Kuehne has exhibited pure visual purple with a trace of neurokeratin in decayed retinæ by subjecting them to trypsin digestion, bile, acetic acid of five per cent., and water, and by purifying the remnants with sal ammoniac and benzol.

Boll having in later articles described the normal color of the retina as a pure red, Kuehne lays great stress upon spectral analysis of the visual purple. The examination is made with a spectroscopic apparatus with double hollow prisms,[2] one of which is filled with the purple solution and the other with colorless bile possessing the same refractive power. In this way the spectrum of the visual purple, which soon passes over into that of the visual yellow, can be rapidly observed. (Fig. 3.) This apparatus

FIG. 3.



a, spectrum of the visual purple; *b*, spectrum of the visual yellow; *c*, solar spectrum. (Kuehne.)

enables the visual purple to be examined in solutions of different thickness. Thin sections exhibit a shading into yellow-green before the *E* line appears, whilst thicker ones show both spectra with diffuse absorption-lines without striated bands.

Retinæ or drops of the purple solution can be examined in the objective spectrum. In yellow-green they appear black up to the beginning of pure violet. In violet they are yellow and orange-gray. In red the retinæ cannot be distinguished from those which are bleached, nor the drops of purple solution from drops of water.

Kuehne has discovered that when the image of a fresh retina in an eye is physiologically blended with a color by one of the methods suggested by Helmholtz, only those colors which are complementary to purple give sensation of neutral gray. He has also found that the retinal color in mixtures of spectral colors (partially white and others) behaves like purple, and that in genuine purple (red and violet) it appears extremely bright; in the pseudo-purple (red and blue) it is fire-red.

Visual purple being a lac dye, but little of it can be seen in the retina in front of the dark pigment of the fundus of the eye. It is somewhat

[1] Ewald and Kuehne, H. U., i. S. 454.

[2] Centralb. f. d. Med. Wiss., 1877, S. 194, and H. U., i. S. 50; also H. U., i. Ss. 139–166.

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better seen in front of the white or yellow tapetum of the dog or the cat, and can be remarkably well seen in fishes with a retinal tapetum (*Abramis brama*), or even through the pupil of the fish when dying in the dark.[1] O. Becker[2] has shown, in opposition to Boll, as well as Dietl and Plenck,[3] that the visual purple cannot be seen in the living human eye.

The visual purple is visible under the microscope wherever the cylinders stand erect, and those that lie obliquely may show a complementary green against the mosaic of the rest. Recumbent rods appear rose-colored when thickly clustered (frog, salamander). In tritons the position for observation is more favorable. This is so because these transition structures between rods and cones contain the purple in a layer of connective tissue.

PHOTO-CHEMICAL DECOMPOSITION OF THE VISUAL PURPLE.

When light acts upon the visual purple (rhodopsin) it first produces visual yellow (xanthopsin) and then visual white (leukopsin). The colors which appear during the bleaching vary according to the entrance of the visual yellow. In daylight the retinal color passes over into redder purple, pure red, orange, yellow, and "chamois," before it entirely disappears. It may pass through pale lilac to total loss of tint. The fresher the retina the more marked is the latter course. The action of light is direct. Protected districts remain circumscribed with color. The bleaching depends on the intensity of the light. No secondary effect of a bleaching once begun has yet been observed. A bleaching that might not be noticeable by itself is recognized when the retina in our own eye is mixed physiologically with white. Fresh retinæ then appear rose-colored; slightly bleached ones, "chamois." This is also so when we observe it in spectrally mixed purple, in which case fresh retinæ appear Flemish purple bleached a dull tile color (a shading off between carmine and cinnabar red).

Examination of the action of the purple by monochromatic light is made with the aid of tinted glasses, or of the colors of the spectrum, in which, for light of short vibrations, flexion-spectra are preferable. All colored light affects the purple more or less, although with weaker tints hours and even days are needed to complete the bleaching. Fresh retinæ extend in their initial portions as far as green before bleaching towards yellow; in their final portions more to lilac, this being so because visual yellow is more rapidly destroyed in these portions than in the initial portions. In a good light, the retina or the purple solution exhibits great alteration. In yellow-green the alteration appears in an incredibly brief period, passing in greenish yellow to indigo in from two to ten minutes, in yellow in twenty minutes, in violet and orange in thirty minutes, in ultra-violet in forty-five minutes, and in red in a little longer period of

[1] Kuehne and Sewall, H. U., iii. 3 and 4, S. 263.
[2] Klin. Monatsb. f. Augenheilk., xv. Jahrgang, S. 145, 1877.
[3] Centralb. f. d. Med. Wiss., 1877, 273.

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time. So far as the action of monochromatic light upon visual purple or visual yellow is concerned, it has been established that the law of the action of time coincides with the amount of absorption, and that light decomposes both of these pigments the more it is absorbed by them. An exception in blue and green light, which is obtained by absorption with colored glasses, in favor of blue, may depend upon differences in intensity between such light and spectral light.

As refrangible light acts with greater effect upon visual yellow, and less refrangible light acts more rapidly upon visual purple, blended light of both sorts is best for bleaching. The most powerful mixture, however, need not appear white. A combination of cyanide blue and greenish yellow to greenish white is the most dangerous for the retina. On the whole, each individual color of such mixture acts for itself, and only better so far as total bleaching of the purple is concerned when it is united with the others. On account of the greater intensity of mingled light, the result of the union is best confirmed by successive mixtures.

CHEMICAL ACTION OF THE VISUAL PURPLE.

Visual purple does not seem to contain iron.[1] Many chemical agents bleach it. This is so even in the dark, and when so bleached it cannot be restored. It is destroyed by lime water and baryta water, alkalies, and most acids. (According to Van Genderen Stort, the retina of the Perca fluviatilis remains red after treatment with thirty-five per cent. nitric acid.) It is further destroyed by alcohol, chloroform, chloral hydrate, acetone, aldehyde, acetic ether, oil of mustard, thymol, oil of bitter almond, oil of turpentine, solutions of soap, subchloride salts, chlorine, sulphuric acid, iodine, and bromine. Some of these act rapidly, others slowly; a few even when greatly diluted. In many, the purple passes through yellow to bleaching. Absolute glycerin acts so far only as to make the purple of dry retinæ yellow. Visual purple remains unaltered in sal ammoniac, carbonates, alkalies, salt solutions of every intensity, alum, cyanide of potassium, sulphuric, subchloride, and nitrogenous alkalies, sulphate of ammonium, sulphuretted hydrogen, ammoniacals, acetates containing solutions of oxide of tin, chloride of iron, acetate of lead, superoxide of hydrogen, ozone, carbonic acid, carbonic oxide, boric acid, hydrocyanic acid, aqueous glyconin, absolutely pure ether, benzol, petroleum ether, carbonic dichloride and tetrachloride, sulphuret of carbon, the fats and balsams, oleic acid, oil of bergamot, santoninic acid and soda santonate, and, finally, urea. Trypsin digestion does not attack the purple in the retina, but only in a cholate solution.[2] On the whole, with the exception of the oxidates of hyperosmic acid and permanganate of potassium,[3] powerful oxidizing and reducing substances have but little effect upon the visual purple.

[1] Ewald and Kuehne, H. U., i. S. 438.
[2] C. W. Ayres, H. U., ii. S. 445.
[3] Dreser, Zeitsch. f. Biologie, xxii. S. 23.

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The visual purple is also destroyed by the influence of higher temperatures. Retinæ are instantaneously bleached at 76° C. (168.8° F.); solutions of purple at 72° C. (161° F.). The lowest temperature that alters the purple is 51° C. (123.8° F.). The addition of sal ammoniac and carbonate of sodium reduces this a little lower. The fact that the purple of retinæ dry or softened in concentrated glycerin or saturated salt solutions is more slowly destroyed by increased temperature is suggestive of that of the coagulation of albumin. Rabbit's purple is earlier destroyed than that of the frog, suggesting a chemical difference between the purple of various animals.

Temperature exerts some influence upon the rapidity of bleaching by light. Frozen retinæ bleach very slowly. In the frog, the sensibility to light increases slowly from 0° C. (32° F.) up to 40° C. (104° F.), though very noticeably from 45° C. (113° F.). Inasmuch as the solution of visual purple obtained from rabbits is much more sensitive to light at 35° C. to 38° C. (95° F. to 100° F.) than at 75° C. (167° F.), it is right to presume from this that the purple of living warm-blooded animals is very sensitive to light.

The chemical influences upon bleaching by light are retarded by the withdrawal of water, without being stopped. Oxidizing and reducing materials exert no influence upon this process. Bleaching seems to be a destruction with loss of water. Retinæ in acetic acid in the light exhibit a greater tendency to yellow than when they are placed in carbonate of sodium. Sal ammoniac does not seem to exert any influence upon bleaching by light.[1] It further seems that in light of short vibrations the visual yellow is more easily produced than it is in acetic acid, whilst in less refrangible light its destruction is delayed.

Under certain circumstances the indolence of the visual pigment is a peculiar phenomenon. Eyes from corpses that have been kept in the dark are often insensible to light, many hours being lost before the visual yellow is totally bleached. As this is generally the case with most animals kept in dark stables, it is curious that visual yellow is not oftener seen. Melloini alone[2] has seen it, and upon this fact he has based a special theory of light. The longer retinæ, especially those that have been separated from the epithelium, have lain in the dark, the more pronounced is the phenomenon: the same occurs after drying. Desiccated purple solution being but slightly indolent, it seems as if it were a question of the fixation of the purple in the rods (perhaps of neurokeratin). Aluminized retinæ, if for a long time dried in the dark over sulphuric acid, become yellow when remoistened, but the yellow is not completely bleached even by the direct sunlight. Retinæ that have become yellow with acetic acid do not, if they have long been kept in darkness, lose their color for days. According to

[1] Compare Kuehne's remark, H. U., ii. S. 446.

[2] Comptes-Rendus, xiv. p. 823, and Ann. de Physik, lvi. p. 574.

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Puglia,[1] various acids (acetic, sulphuric, and nitric) produce a more constant yellow. In solutions of sublimate the retina seems to assume a bright yellow which is unalterable by light. Under certain circumstances thawing furthers this indolence.

THE RELATIONS OF THE FLUORESCENCE OF THE RODS TO THE VISUAL PURPLE.

The whitish-green fluorescence of the retina discovered by Helmholtz[2] and further investigated by Setschenow[3] originates from the layer of rods,[4] and is connected with the visual purple and its bleaching. The whitish-blue fluorescence of the anterior layers of the retina is independent of the action of light. In man and animals, fresh retinæ fluoresce pale blue, and bleached retinæ fluoresce greenish. Rods without purple in the region of the ora serrata show scarcely any fluorescence. Cones without purple act in the same way. The fovea centralis in ultra-violet appears as an increasingly darker spot the more the surrounding rods fluoresce. A retina deprived in life of its purple fluoresces greenish white posteriorly. It is difficult to say whether the visual purple itself fluoresces, since cholate solutions also fluoresce bluish. Purple dissolved in cholate-acid alkalies appears pale blue in ultra-violet. After bleaching by light it becomes a bright greenish blue.

When the yellow disappears, or when it has hardly become yellow, or when visual white has been formed with small clumps of purple, the layer of rods is most fluorescent (very green). Visual white is evidently a greenish fluorescent substance. Visible yellow does not possess this property, or at least possesses it to but a slight degree. Chloride of zinc increases fluorescence, tinting the retina yellow in the dark and then depriving it of its fluorescence. If the retina is now illuminated till it bleaches, the fluorescence reaches its maximum. Acetic acid acts in the same manner.

Fluorescence ceases on moistening with alcohol or caustic alkalies. If the alcohol is applied when the rods are bleached by light, the fluorescence is retained. Alcohol does not seem to alter the visual white, but from visual purple it appears to produce different alterations that are connected with discoloration from those that are produced by light.

The green rods discovered by Boll were found by Ewald and Kuehne in the turtle-dove. They are identical with the rods provided with short external processes that have been described by Schwalbe. They are more slowly bleached by light than the purple ones, but at last, as far as light extends, this occurs totally. It is not yet known whether they are pigmented or not.

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[1] Sulla Porporo visuale, Annal. d. Ottal., vii. 568, and Gaz. Méd. de Paris, July 12, 1879.

[2] Ann. d. Physik., xciv.

[3] Arch. f. Oph., v. 2.

[4] Ewald and Kuehne, H. U., i. S. 169.

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PIGMENTS OF THE CONES.

The outer members of the cones are never tinted; pigment has been discovered only in the inner members in birds, reptiles, and a few fish.[1] In man and the ape the fovea centralis is never pigmented.[2] Horner's observation[3] of an evanescent cherry-red spot in the fresh eye cannot refer to coloration of the fovea itself, but must depend upon transmitted light. The yellow pigment of the macula, which in Max Schultze's opinion lies in front of the visual cells, disappears after a few days' exposure to the sun.

The oil globules discovered by Hannover[4] on the border between the inner and outer layers of the cones have been carefully studied only in hens and pigeons. They are purple to red, orange-yellow, and greenish-yellow. Occasionally they are pure green and blue. They consist of fat, with pigment in solution. Kuehne and Ayres[5] have isolated three pigments from the oil globules,—chlorophane, xanthophane, and rhodophane. Kuehne thinks that there is a fourth,—kyanophane.[6] These investigators exhibited the pigments by saponification in alcohol, the next best identification being based upon the exclusive solubility of chlorophane in petroleum ether, with a superfluity of alkali, and the insolubility of rhodophane in alcohol in the presence of acids or ammoniac. These pigments, when pure, are soluble in ether, petroleum ether, chloroform, sulphuretted carbon, and fatty oils; also in alcohol, with the exception of rhodophane, which is soluble there only in the presence of acids and ammoniac. Rhodophane is soluble in acetic ether. All the pigments are insoluble in water, alkalies, and ammoniac. Chlorophane is greenish yellow, soluble in alcohol and in ether, giving them the same tint; in sulphuretted carbon it is orange-yellow. When evaporated it is soluble in alcohol and in ether, with the same tint as before. Xanthophane dissolves in alcohol and in ether, leaving an orange-yellow tinge. In sulphuretted carbon it becomes reddish orange. Rhodophane dissolves red in chloroform; in sulphuretted carbon it becomes violet. The three pigments give characteristic spectra. (Fig. 4.)

Wälchlis's[7] doctrine, that chromophane is a post-mortem product, and Capranica's,[8] that the three pigments are identical, have been refuted by Kuehne.

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[1] Leydig, Lehrb. d. Hist., also in the *Bombinator igneus*.

[2] Kuehne, Centralb. f. d. Med. Wiss., April 24, 1877, S. 109, and H. U., i. Ss. 34, 105, 109, and H. U., ii. Ss. 69, 89, 378; later confirmed by Donders, Klinisch. Monatsbl. f. Augenheilkunde, xv. Jahrgang, S. 156.

[3] Klinisch. Monatsbl. f. Augenheilk., xv. Jahrgang, S. 156.

[4] Archiv f. Anat. u. Physiol., 1840, S. 320; 1843, S. 314.

[5] H. U., ii. S. 341.

[6] H. U., iv. S. 246.

[7] Graefe's Archiv f. Augenheilk., xxvii. 2, S. 303; xxii. Jaar. Vers. b. h. Nederl. Gasth. v. Ooglijders, S. 153; Donders, Utr. Phys. O. Lab., vi. S. 297.

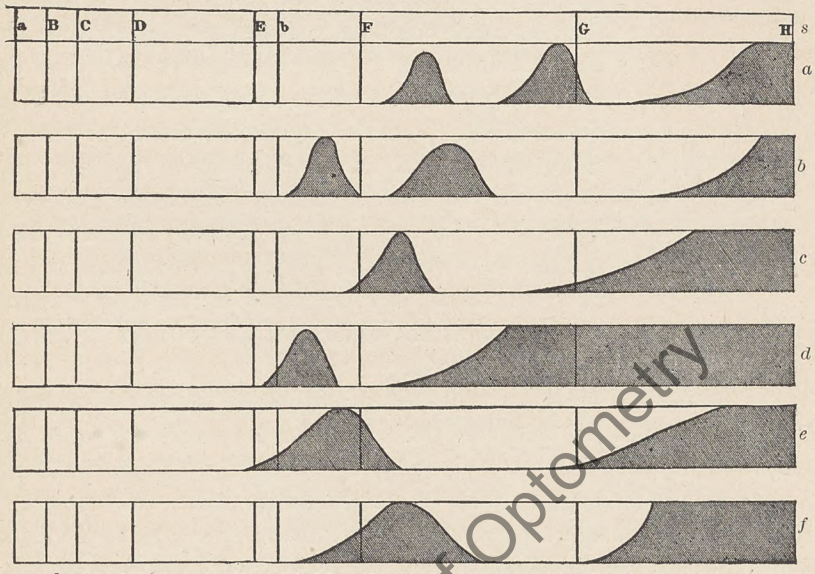
[8] Loc. cit.

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According to Capranica (modified by Kuehne), the oil globules and chromophanes become blue in nitric acid and concentrated sulphuric acid. In nitric acid containing nitrous acid they become a bluish green. Rhodophane is affected least of all. The greenish-blue to blue reaction with iodine, discovered by Schwalbe in the summits of the cones, is not seen, according to Kuehne, in pure pigments. The chromophanes are not entirely immutable in the dark. They are most stable in the presence of alkalies and after removal of their genuine vehicle, the fat. In solutions of chloroform they are most sensitive to light, and least so in sulphuretted carbon and when slightly acidified.

It happened to the author to discover that pigeons' retinæ, when enclosed

FIG. 4.



s, solar spectrum; *a*, spectrum of chlorophane in ether or petroleum ether; *b*, spectrum of chlorophane in bisulphide of carbon; *c*, spectrum of xanthophane in ether; *d*, spectrum of xanthophane in bisulphide of carbon; *e*, spectrum of rhodophane in benzole; *f*, spectrum of rhodophane in oil of turpentine. (Kuehne.)

in carbonic acid, bleach more slowly than in air;[1] but this may be an action of acid. Ozone bleaches the chromophanes in the dark,—chlorophane most rapidly, rhodophane the slowest.

The pigments, which so frequently occur among invertebrates that they are regarded as rudimentary eyes, are, according to Kuehne[2] (partly in opposition to Chopin's views[3]) and Krukenberg,[4] but slightly sensitive to light.

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[1] H. U., loc. cit.
[2] H. U., i.
[3] Comptes-Rendus, xxv. p. 447.
[4] H. U., ii. S. 58.

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ALTERATIONS IN THE RETINA DURING VISION.

Frogs held for ten to fifteen minutes towards full sunlight, or rabbits with enlarged pupils kept for a time in the light, show colorless retinæ. Bleaching of the visual purple is, therefore, an effect of light, but in its course significant variations arise from the condition of things in isolated retinæ.

The best proof of the direct local action of light is that the images thrown by the refracting media on the fundus, when well defined, leave well-defined designs in the purple layer of the rods,—photographs, as it were, or optograms. (Fig. 5.) Optograms can be obtained in the eyes of fresh rabbits or cattle by placing them in a black box twenty-five centimetres high, covered with a ground-glass plate provided with black stripes four or five centimetres wide and the same distance apart. The experiments are made in the open air. After an exposure of from two to seven minutes, according to the intensity of the light, the retinæ are prepared before a sodium flame, laid overnight in a four per cent. solution of alum, and then shelled out over small glazed porcelain cups, where they can be at once examined by daylight or after drying. Where many experiments are to be made, it is best to have a darkened room with a movable shutter.

FIG. 5.



Rabbit's retina containing visual purple.—*a*, stripe containing medullary nerve-fibres; *b*, the visual ridge; *c*, optogram. (Kuehne.)

There are many difficulties in the way of exhibiting optograms in frogs' eyes, the alum treatment being useless. In order to remove the retina uninjured, the optic insertion has to be excised. Another difficulty lies in the pigment epithelium clinging to the exposed locality (epithelial optogram), so that either the image must be made minute to keep the epithelia in continuity, or a long exposure in very moderate light must be obtained. The best plan is to make the frogs œdematous by letting them, when curarized, remain for some time in water. Pseudo-optograms occur in the frog when the rods strip off from the illuminated spot and only the cones remain, thus producing white designs. Genuine optograms are characterized by the exhibition of bleached rods under the microscope. By following these suggestions, optograms which under one hundred diameters are scarcely diffuse may be obtained.

Optograms obtained in rabbits, with stripes five centimetres in breadth, and at a distance of twenty-five centimetres, are one and a half millimetres wide. In frogs with an object distance of fifteen centimetres, they are six-tenths of a millimetre wide.

The course of the photo-chemical process is best followed when it is arranged that the optograms in rabbits shall fall partly upon the tinted visual stripe and partly on both sides of it, as the various stages of the bleaching can then be compared. Furthermore, the images ought to fall

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upon that portion of the retina which lies below the horizon, because it is better tinted and does not contain medullary nerve-fibres.

The changes of color in the living retina run through the same intervals as in the isolated retina,—pure red, tile-red, orange, rose, chamois, yellow. Care in the time of the exposure produces colorless stripes with purple cross-bands of equal width (as in the object). If the eyes are exposed for too short a time, pure red stripes on a purple ground are obtained. If they are exposed too long, colorless stripes on a pure red ground (for the optograms occur precisely on the visual ridge at the stage of exact exposure) are obtained. Later, colorless stripes and yellowish ones, which always grow narrower, are seen.

Kuehne found that the action of monochromatic light upon the purple, in life, varied in many respects from what Boll had asserted. Its intensity, for instance, is less than that of white light. Well-isolated spectral colors or colored glasses or solutions whose tints must be verified by the spectral apparatus are employed. Whilst Boll had at first believed that no monochromatic light could totally bleach the retina, he later granted it for light with short vibrations, assuming various stages, which remind one of the shades of light employed in bleaching. So far as yellow was concerned, he conceded that it contained pure red, which he regarded as the normal color of the retina. He asserted that common red deepened it to a brownish-purple. Ewald and Kuehne, on the contrary, discovered that all colors discolored the retina, though with different degrees of rapidity. Red, for example, in frogs, in the height of summer discolored in two hours, yellow-green in half an hour or more. This latter, however, is difficult to recognize, on account of the obstinate adherence of the pigment epithelium. Even in frogs with curare œdema, pigment existed between the rods, and produced what Boll had regarded as its characteristic discolorations.

Finally, Kuehne and Ewald have advanced the following theories:

1. Photo-chemical decomposition in the isolated as well as in the living retina originates a single pigmented product, the visual yellow, the proportion of which to the still undecomposed purple decides the retinal color before the bleaching by light is terminated.

2. Where the visual yellow is decomposed as rapidly as, or even more so than, the visual purple (in light of short vibrations), the retina becomes rose or lilac. Where the opposite occurs (in light of long vibrations), the retina becomes in turn red, orange, chamois, and yellow.

Having discovered the influence of oxygen upon the bleaching of the chromophane, and the oxidation in the living body proceeding with an intensity that under equal chances could not be chemically imitated, the author felt the need of investigating how this substance, which is slightly sensitive to light, behaved during life. Kuehne has shown[1] that after removing the cornea and lens in birds the pupil can be kept open by a speculum

[1] H. U., ii. S. 89.

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without loss of vitreous, and the eyes illuminated for hours with a heliostat. In pigeons, the result is entirely different from what was expected. The colors of the tips of the cones are deepened, and some become brighter. The yellowish-green inclines to green, the red to rose and ruby red. The xanthophane tips do not change at all. The inner members of the cones with chlorophane tips often contain deposits of a diffuse, finely granular, yellowish-green pigment, which is never seen in animals that have been kept in the dark. In two examples of *Butea vulgaris*, one of which was kept in the dark, whilst the other remained in the light, Kuehne found in the former the tips of the cones colorless, red, orange, and yellowish green of moderate saturation. In the latter, none were colorless, and, except a few of deep orange and dark red, none were greenish yellow and only a few were bluish green. All these discoveries impress us with the idea that chromophane is a neoplastic formation that is due to the action of light. At most, the cone-tips may have a yellow pigment which yields slowly to light.

The oil globules of the epithelium containing lipochrin exhibit in the frog, after exposure to bright light, a peculiar segmentation into smaller and brighter globules which is chemically different from the myeloidin granules. The latter vary so much in frequency that it is difficult to decide how they act under illumination, but their appearance and disappearance seem to be connected with processes which ensue upon illumination of various length and intensity. The peculiar appearance of striated and bristly contents of the epithelial summits of eyes exposed to the light is probably due to bleached fuscin.

REGENERATIVE PROCESSES.

All the rods that are bleached by vision resume their maximal color when the eyes have been kept sufficiently long in darkness. The purple from frogs, which had in life been totally bleached, is completely regenerated in the course of three hours in complete darkness, no matter whether the eye remains in the living creature or is enucleated. In either case, the restoration passes through pale lilac and rose to purple. Even the halves of frogs' eyes from which the vitreous has been removed are partially regenerated. The regeneration is produced by the retinal epithelium; for when two living frogs are bleached, one of which is in a state of curare œdema, so that the retina peels off without the epithelium, and the other animal is not curarized, so that the epithelium clings to the retina, the purple is restored in the second retina, but not in the first. In this regeneration lies the reason for the difference between the time required for bleaching the living retina, or the retina remaining *in situ* after life, and that required for bleaching the isolated retina. It also accounts for the apparent indolence of the purple in life, which is greater in the frog than it is in warm-blooded animals. This epithelial function can be well shown by elevating the retina one-half (without its epithelium) and then exposing the eye to the light;

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the elevated half after removal of the retina is colorless, the other half remains red or yellow. The swifter bleaching of the isolated retina is not due to cadaveric processes, but is dependent upon the absence of regeneration. The epithelium, however, must be alive, or in a state of existence, to produce regeneration; for if a frog's eye be destroyed in the dark in water at a temperature of 45° C. (113° F.) the bleaching will be as rapid as in an isolated retina; or if the frog be dazzled whilst alive to the point of bleaching the retina, and the eye destroyed in a similar manner, regeneration will be absent. It is not necessary to regeneration that the retina should remain in its natural connection with the epithelium, for it may be half detached, or detached to the zone of Zinn, or it may hang down like a sac filled with vitreous, or be removed *in toto* and bleached and again restored to its place whilst regeneration still remains perfect. In the first case, both halves of the retina will exhibit the normal tinge of purple without any line of demarcation. When, however, the rods are bleached in life, the purple is not regenerated in this manner.

It is difficult to be convinced of any traces of regeneration in warm-blooded animals, in which the epithelium rapidly dies. By working quickly, however, it can be seen that the same bleaching-time as in life produces at once, and for a few minutes after death, optograms that are successively more and more developed. This is so because even in life, and for a short period after life, regeneration retards the bleaching process. So in albinotic rabbits in which the folded fundus of the eye can still be seen, the visual purple, and the coloring matter of the blood, pieces of retina removed directly after enucleation bleach much more rapidly than those that remain protected by regeneration in the eye. This distinction disappears after ten minutes in the dark.

It is worth noticing that regeneration in living animals occupies a very long time. Coccius has observed[1] a remarkable pallor of the retina in rabbits which had remained for a long time in the open air and then a half-hour in darkness. Ewald and Kuehne have established, by means of the optographic method, that regeneration in the frog begins after twenty minutes and is completed in from one to two hours (longer still if the temperature is low). In rabbits the same steps require but seven minutes and thirty minutes respectively.

These variations in regeneration or rhodogenesis have recently been explained. Retinæ that have been bleached to loss of all color, or even longer in life, do not show visual yellow, but exhibit lilac, rose, and purple in any stage of regeneration. In life, the products of bleaching are swept away. That this is so is suggested by the circumstance that retinæ bleached in life do not fluoresce whitish green, and the purple must be formed anew, which happens in the sequence of colors previously mentioned. This process has been called neogenesis. Furthermore, and particularly in iso-

[1] Acad. Program., Leipzig, 1877.

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lated, bleached retinæ, and in life, with even a weak illumination, another regeneration of the bleaching products that have not been swept away occurs in the usual succession of colors,—yellow, chamois, orange, red, purple. This is called anagenesis. Both processes are recognizable by optograms according as they are produced by longer or by shorter illumination. Neogenesis is slow, anagenesis is more rapid. In this way the differences in regeneration can be explained. The occurrence of rapid anagenesis in life also is proved by experiments with intermittent light, which give either no optograms at all, or imperfect ones. This will occur if in the pauses of about three-quarters of a second between the individual irritations of light the purple can be again restored from its bleaching products.

There is still another regeneration which is independent of the life of the cells. This is known as auto-regeneration. Attention was first called to it by the fact that the dependent portions of retinæ free from fuscin bleached more slowly, as if they were preserved from decomposition by something that was flowing from above upon the purple. In the dark, every isolated bleached retina shows a certain return of color, which process can be repeated several times. The retina may be actually dead, and yet the auto-regeneration still persist. Even bleached-out solutions of purple show a slight but undeniable return of color, and an artificial rhodogenesis can also be discovered.[1] Inasmuch as solutions of retinæ bleached during life and separated from the epithelium by curare œdema do not color in the dark, a rhodophylactic property must be attributed to the epithelium. It would be also necessary to conclude that it contained a substance called rhodophane, if the regeneration of solutions of purple could be increased by solutions of epithelium. This, however, would meet with technical difficulties, since epithelial solutions can hardly be obtained without hæmoglobin. In addition, together with blood-pigment they also exhibit a purple the bleaching and regeneration of which can be easily followed. In fact, it seems as if the neogenetic purple were here formed. Nevertheless, in frogs kept on ice in the dark, we succeed in obtaining from the retina and epithelium, with bile, extracts of purple that are free from hæmoglobin. When these are compared with extracts obtained from the retina alone, a slower bleaching and a more rapid and intense return of the color in the dark are found in the former. There must, therefore, be a rhodophyllin which is soluble in bile.

The slight exudation of material attributed to the epithelial cells may explain the slowness of neogenesis, whilst the illumination itself seems to delay the process, because the illuminated and naked epithelium has less capacity than before of recoloring the rods. So long as the light reaches the epithelium through the purple rods, the latter cause has less foundation, since moderated red light, as shown by experiments on rabbits and frogs, does less harm to the regenerative process. This, however, is the case only

[1] Ewald and Kuehne, Centralblatt f. d. Med. Wiss., 1877, S. 753; H. U., i. S. 248.

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after illumination of the rods in which the neogenesis first begins in its full extent.

Regeneration in warm-blooded animals seems to cease either with the circulation of the blood, or a little later. It is retarded by pressure upon the eyeball, by excessive loss of blood, and by violent electrical shocks which contract the blood-vessels. It is not influenced by stimulating or paralytic conditions in the nerves of the eye. Holmgren [1] has demonstrated the visual purple in rabbits, and Langendorf [2] the same in frogs, in all of which the optic nerve had long before been severed. Rabbits prepared by Holmgren's method are said to exhibit normal bleaching and regeneration for a long time.[3] Division of the trigeminus or of the cervical sympathetic or of the oculo-motorius in the skull has no effect on regeneration; nor is there any difference after large doses of curare or atropine. Irritation of the second eye by light or illumination of adjacent regions fails to show any change in the normal course of the process. On the contrary, small doses of muscarin and pilocarpine, which increase glandular activity in the dog, rabbit, and frog,[4] hasten regeneration, so that the epithelial cells must possess secretory activity.

THE IMPORTANCE OF THE PHOTO-CHEMICAL PROCESS FOR VISION.

A number of photo-chemical processes in the eye, a part of which are very rapid and a part rather slow, have now been described. This knowledge has led to the establishment of a photo-chemical hypothesis which is intended to explain the actual course of these processes. The hypothesis assumes the existence of photo-chemical, decomposable, visual matters [5] in the visual cells, which do not cause excitation so long as they remain undecomposed. The moment they are decomposed by the action of light they give off products which are to be regarded as exciters of vision. When the secondary action of light is considered, a material view of the excitatory matter seems to be the preferable one. In accordance with this, the irritation is supposed to be produced by transformatory processes,[6] which cease when the light is removed.

Any matter to be rightly called visual matter must lie in a situation where there is reason to place the excitation by light,—*i.e.*, in the visual cells. It must also be proved that this matter can be altered by light during life, and that a slight transformation may be of great significance. Nevertheless, there is no compulsion to regard any matter with such peculiarities as visual matter; and, in fact, even visual purple may be nothing

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[1] H. U., ii. S. 81.

[2] Archiv f. Anat. u. Phys., Phys. Abth., 1877, S. 437.

[3] Ayres, H. U., ii. S. 215.

[4] Ayres, loc. cit; Dreser, loc. cit., S. 30.

[5] This name was first used by Exner, Arch. f. d. Gesammt. Physiol., xvi. S. 409.

[6] Bernstein, Unters. u. d. Erregungsvorgänge in Nerv- und Muskelsystem, Heidelberg, 1871.

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more than a mere absorber of light. From this point of view, it is important to know that vision can take place without visual purple. Moreover, visual purple does not exist in the cones in the fovea centralis with which we see best. Further, animals that have been deprived of the purple do not act differently from those which possess it. Frogs without the purple search for their favorite color, green; and rabbits, which seem to have no cones or visual cells with or without purple, see well with yellowish rods. Yet it is not justifiable to deny that purple may be a visual pigment simply because it is impossible to tell whether the vision of animals with bleached-out retinæ is modified in any particular way. Personal observations would help to an opinion in this respect if it could be decided when our own visual purple (which, from Kuehne's experiments, is very resistant in life) had disappeared. Unfortunately, this cannot be demonstrated with the ophthalmoscope, and the possibility of perceiving the purple entoptically, which was unknowingly done by Tait,[1] later suspected by Boll,[2] and more accurately described by Ewald,[3] is of but little utility, because the experiment is successful only under special conditions. Vision without the purple, and mostly without retinal pigment, renders it certain that this visual matter is only a paradigm for other untinted matters which must act in a similar manner,—*i.e.*, as exciters of vision by the decomposition of light. The great difference between the intensity of the irritation in the visual organ must lead us to suppose that the sensibility to light of these untinted matters varies.

Exner believed[4] that he discovered in his own eye the presence of visual matter, which disappeared after stopping the circulation by pressure on the organ. When Kuehne objected[5] that this phenomenon might just as well be due to alterations in the conducting apparatus, especially of the gray substance of the retina, Exner replied[6] that there was no proof in favor of either view, and endeavored by new experiments to support his former hypothesis.

MECHANICAL ALTERATIONS IN THE RETINA PRODUCED BY LIGHT.

1. *The Pigment Epithelium.*—The sliding off of the retina in illuminated frogs' eyes, first seen by Exner, during decomposition, or even when covered with epithelium, does not depend on changes in consistence or softening, as Boll thought, but upon the mobility of the protoplasm of the retinal epithelial cells and their prolongations, as suggested by Czerny.[7] Kuehne had found that it depended on migration and shifting in the

[1] Edinburgh Proceedings, 1869–70, vii. p. 605.
[2] Arch. f. Anat. u. Physiol., Phys. Abth., 1877, S. 4.
[3] H. U., ii. S. 241.
[4] Pflueger's Archiv, xvi. S. 407.
[5] H. U., ii. S. 46.
[6] Pflueger's Archiv, xx. S. 614.
[7] Sitzungsber. d. Wiener Akad., lvi.

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stratification of the crystals of fuscin,[1] in connection with and depending upon the amount of the illumination. He later[2] studied the phenomenon more closely, and Angelucci has also offered some opinions concerning it.[3] Illuminated retinæ remain slightly covered with epithelium, whilst those without pigment and kept in the dark slide off.

There are other circumstances which must be taken into consideration so far as the adhesion of the epithelium and the subdivision of the pigment are concerned. For example, a quarter or half an hour after death a firmer adhesion is developed, during which the pigment wanders forward in small portions as far as the external limiting membrane. This is developed, even in frogs that have been kept in the dark, by lower temperature without migration of pigment, and is even stronger than curare œdema. The latter loosens the epithelium at 30° C. (86° F.), but makes the separate fuscin-needles project considerably. The prolongations of the cells are easily torn from their roots. Œdema also produces loosening in fishes with bleached rods when exposed to the sun, in which case only small masses of pigment remain between the rods. Fick has called attention to the influence of suffocation, to which the writer will later return. These

FIG. 6.



Shifting of the fuscin in the frog's retina.—*A*, in the dark; *B*, after the action of sunlight. (Kuehne.)

conditions must be kept in mind when we are observing the migration of fuscin under the influence of light. The retinæ of frogs that have been kept in the dark loosen easily and completely from the epithelium, but the fuscin projects between the rods to one-third or one-half of their height.

The epithelial cells exhibit short, dark, ninepin-shaped processes which terminate in long, fine fibres without pigment and without bulging at the end. The base of the cells is filled with pigment, which extends to the anterior margin of the nucleus, but on the summits rises into a slight eleva-

[1] H. U., i. Ss. 21, 101.

[2] H. U., i. S. 370.

[3] Atti d. R. Accad. d. Lincei, 3 Serie, 28, 1877–78; see also Arch. f. Anat. u. Physiol., Physiol. Abth., 1878, S. 352.

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tion. The summits of the rods in retinæ in which the epithelium has not slid off (cooling off) have but little fuscin.

The epithelial layer is firmly adherent in illuminated frogs; thick ropes and spindle-shaped masses of pigment rise up among the rods. The base of the cells has lost much fuscin, but the pigment covers the summits of the rods more extensively. In this way, with pigment in the base and spindle-shaped projecting clumps between the rods, we see, as it were, a double zone of pigment. Swelling of the pigment-cells processes and of the rods makes the epithelium adhere. After an hour or two in the dark, we discover the maximal position for darkness,—that is to say, in about the same time that it is necessary for neogenesis of the purple. Moderate light enables us to see that migration of the pigment begins before the purple is bleached, whilst all illuminations which make any permanent demands upon the regeneration and are most favorable to equilibrium between the bleaching and the restoration of the purple act most forcibly upon the epithelium. The direct relation between the illumination and the migration of pigment is best shown by the epithelial optograms seen in frogs after a brief but brilliant illumination. The migration of the fuscin is most marked in red light, especially in such intensities as leave the fuscin normal, whilst migration decreases considerably when permanent bleaching is attained. The actual migration of the fuscin into the protoplasm of the cells is best seen in fish[1] in which there is a tapetum, first described by Bruecke,[2] in a certain position of the retina. It is composed of a deposit of guanin in the retinal epithelial cells. Guanin does not migrate under the influence of light, but is always seen in the same permanent form of cells, whilst the fuscin, mostly granular in these cells, migrates in the usual manner. The reason that guanin does not migrate may be that it is situated in a firmer portion of the protoplasm.

Epithelial reaction is probably common to all vertebrates, and also to man, but it is not always easy to observe. Similar processes have been seen in invertebrates in their complicated system of pigment-cells, as, for instance, by Exner[3] and Szczawinska[4] in crustacea, and by Rawitz[5] in cephalopods.

2. *The Rods and Cones.*—In this layer we must first call attention to the swelling of the rods, as suggested above, and carefully studied by Hornbostel.[6] This may be so extreme that the rods lie flat against one another. When restored to darkness, they diminish in size in an hour or more. The swelling is not noticed in red light until the purple has totally disappeared.

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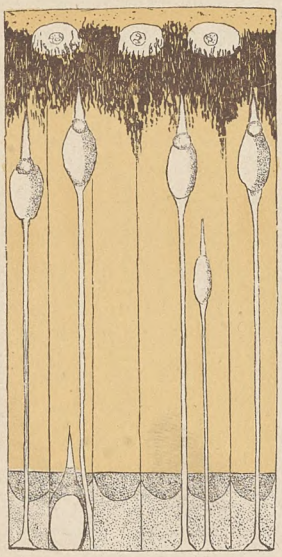
[1] Kuehne and Sewall, H. U., iii. 3 and 4, S. 221.
[2] Mueller's Archiv, 1845, S. 387.
[3] Sitzungsber. d. Wiener Akad., Naturw. Abth., xcviii., March 3, 1889.
[4] Loc cit.
[5] Zool. Anzeiger, No. 363, 1889, S. 157.
[6] H. U., i. S. 409.

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A much more remarkable sight is the shifting of the cones under the influence of light, as described by Van Genderen Stort,[1] in frogs which had been kept for four hours in the dark and whose retinæ had been hardened by Altmann's method[2] with three and a half per cent. of nitric acid. Here the pigment fell back and the cones no longer rested with a broad base upon the limitans externa, but were higher up between the external members of the rods. Fearing that these were artificial productions, he verified the condition with other methods and convinced himself that similar results were always to be obtained, depending upon the rapidity with which the specimens were hardened.

Stort discovered that this change of position was due to the protoplasmic

FIG. 7.



Position of the cones and of the pigment in frogs kept in the dark. (Engelmann.)

FIG. 8.



Position of the cones and of the pigment in the illuminated frog's eye. (Engelmann.)

portion of the internal member (the so-called cono-myoidin) which expands in darkness and contracts in light. He then described the process in the frog, triton, Perca fluviatilis, and Columba Livia, and sketched it in the pig. In the frog and in the perch the difference in the position of the cones is very great, though not the same in all the cones of the same individual. In these animals the expansion is often so great that the outer members of the cones may be higher than the rods. In other animals the change is less.

[1] Engelmann and Van Genderen Stort, Procès-verbal d. k. Akad. ti Amsterdam, March 29, June 28, 1884; Engelmann, Donders, Phys. Lab., Utrecht, iii., Reeks ix. Ss. 141, 142, 145, 1884; and Pflueger's Archiv, 1886, S. 498; also Van Genderen Stort, Arch. Nederland., xxx., 1887, Donders, Physiol. Inst., Utrecht, iii., Reeks x. S. 183, 1887; and V. Graefe's Archiv, xxiii., Abth. iii. S. 229, 1887.

[2] Arch. f. Anat. u. Physiol., Anat. Abth., 1881, S. 219.

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Engelmann found the process slight in the Tropidonotus, and doubtful in the Testudo græca, and thought that the displacement probably occurred in man.

Van Genderen Stort's investigations further show that in the case of twin cones only one migrates, the larger internal member remaining motionless. An exception is to be noted in the twin cones of the perch, where both are of the same size and the protoplasmic portion is common to both. Here the twin cones stretch *in toto* in the darkness and contract in the light. So, too, in the rods, Stort describes a slight motion in opposite senses in various animals. In the perch he acknowledges only that the internal members of the rods probably swell in the dark, and in this way are drawn as a whole centripetally, whilst in tritons the rods are pushed in the darkness centrifugally by anterior migration of the granules of the rods, which in the darkness project a few microns above the limitans externa.

According to Engelmann, the rapidity of the reaction is so great that in frogs kept in the dark the action of even a few minutes of bright diffused daylight is sufficient to reduce to a minimum extreme elongation of the rods; if the light is dazzling, the action is more rapid still. The elongation in the dark is slower, and not always simultaneous with the migration of the pigment. Refrangible rays seem to act more powerfully than others. Since green light in the pigeon most powerfully contracts the rods with red summits, in which case but little light falls upon the exterior members, the locality of the irritation must be sought for inside of these; and since the cones in the inner layer, which possess both red globes and finely divided red globules, contract less in green light than the cones which are free from pigment, the locality of the irritation must be placed in the internal members. It is plain, too, that absorption in the globes and globules cannot produce the irritation, because the reaction is seen in cones without a ninepin-shaped summit, and is absent in turtles, which have intensely colored summits. The contraction in the frog happens first in the inner portion and the elongation first in the outer portion of the inner member. In the pigeon it is more nearly uniform.

If but one eye is illuminated, the cones and pigment in both are in the position for light. The same occurs in beheaded frogs if the brain is preserved. The cones assume of their own accord at a later date the contracted form, like other contractile tissues under spontaneous dissolution. After the brain is destroyed, the action is limited to the illuminated eye. Frogs with bandaged eyes, in which the skin alone is illuminated, show the cones and pigment close to the limitans, in which case the action upon the pigment-cells is more prompt. Strychnine and tetanization of the eye with induced currents in the living animal, or directly after extirpation of the organ, produce in the dark the light-position of the cones and of the pigment. Curare has no influence. Hamburger has confirmed[1] the influence of light

[1] Festbundel F. C. Donders, Amsterdam, 1888, p. 285.

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and darkness upon the cones five months after division of the optic nerve. According to Gradenigo,[1] the external granules elongate when illuminated, and in the eye of a frog kept in the dark and warmed to 35° C. (95° F.) the inner members of the cones and rods were contracted. A. E. Fick found[2] that the position of the cones and pigment for light has changed in the dark after suffocation, and refers the results found in Engelmann's experiments on frogs with bandaged heads to the same condition. He has also reported[3] that some fishes after exposure to the direct sun show the light-position after several hours in complete darkness. If Fick desires to conclude from this experiment that these processes are chiefly indirect, that they have nothing directly to do with the sight, we must once more refer to Kuehne's proof of the direct action of light upon the migration of fuscin (epithelial optograms), and ask him to remember that, even if other irritations can produce the same phenomena, irritation by light is not excluded.

ELECTRICAL PROCESSES IN THE RETINA PRODUCED BY LIGHT.

Holmgren[4] first observed the photo-chemical reaction of the retina. He thought that he could best obtain the retinal induction-current by making connection between the cornea and the posterior portion of the globe, since the termini of the visual cells are turned towards the latter, whilst to the cornea the longitudinal sections of the optic nerve are conducted through the indifferent conductors the vitreous and the lens. In this manner Holmgren found the cornea positive in relation to the posterior portion of the eyeball. He further found that the current fluctuated under the influence of light,—in the frog, for example, it being positive to oncoming or departing light. He also succeeded in demonstrating the same phenomenon in the isolated retina, and in reptiles and mammals he established a negative fluctuation to oncoming light and a positive one to departing light.

Dewar and McKendrick[5] passed the induction-current through the cornea and the optic nerve, finding the same reaction as Holmgren, and also studied the influence of light in various animals. They insist that warmth must be avoided, and thus discovered for the influence of light alone the following conditions: for extirpated eyes of animals, with oncoming light, sinking of the current; with departing light, slight sinking or else no change; for frogs, with oncoming light, an increase; during the light, a slow sinking, oftentimes below the induction-current; on removal of the light, an increase; for living birds and mammals, in oncoming light, a sinking; in

[1] Wien. Med. Zeitsch., 1885, Nos. 28 and 30; Mittheil. a. d. Embryol. Institut v. Schenk, 1886.

[2] Vierteljahressch. d. Naturforsch. Ges. z. Zürich, Jahrg. xxxv., Heft i.

[3] Bericht. d. Oph. Gesellsch. z. Heidelberg, 1889.

[4] Upsala, Läkaraförenings Förhandlinger, Bd. i, 1866, S. 184, Bd. vi., 1871; H. U., iii. 3 and 4, S. 278.

[5] Trans. of the Royal Society of Edinburgh, xxvii., 1874, p. 141.

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prolonged light, a slow increase; in departing light, a sudden increase; for fishes, in oncoming light, an increase; during illumination, at first stationary, then a slow decrease; in departing light, a rapid decrease. Very weak light, like moonlight, sufficed to produce the fluctuations. Lethal doses of curare, santonin, belladonna, morphine, and Calabar extract did not destroy the fluctuations to light. In the compound eyes of crustacea the current was in the opposite direction, but it reacted in the same manner to light.

Kuehne and Steiner elevated the examination exercised off-hand by Holmgren upon isolated retinæ to a method;[1] for, though the investigations previously made had revealed the insignificance of the anterior segment of the eyeball, the examination of the isolated retina still remained open for the decision of the question of the situation of the current. To do this the greatest care in reference to the constancy of the unpolarizable electrodes has been found necessary. This has been obtained by the employment of tissues which had been hardened in alcohol and then washed, and by avoiding the alkaline vapors of the sodium flame by working behind red glass. The induction-current of the isolated retina acted as follows. The optic nerve section was positive on the side towards the rods, in opposition to the periphery. Two points of the latter gave weak variable currents on the fibrous side. The optic nerve section was negative in opposition to every other region. The conduction that proved most suitable for the investigation was from the side of the rods and fibres, and in this case a stronger current, which passed by cathodal arcs from the side of the fibres to the side of the rods, was revealed. This current gradually sank to a medium height, where it generally remained constant. In some cases it would sink farther, die away, and even return. In the opinion of Kuehne and Steiner, the variations of this current to the irritation of light are the same whether the rod side or the fibre side is illuminated. They consider that the radiating heat is not of much account.

Even extremely weak light, like that of fluorescing powder or that produced by a puff at a cigarette, suffices to cause variations. Cold, heat, chloroform, chlorate of sodium, large amounts of pilocarpine and salicylate of sodium, destroy the electric reaction of the retina to light. Atropine and curare do not have any effect. Cutting off or admitting light produces but slight variations. The behavior of these fluctuations to the irritation of light, as careful performance of the experiment shows, is astonishingly constant and complicated.

With the frog's retina sudden oncoming light primarily produces a positive fluctuation, which rapidly attains its maximum. This is followed by a rapid retrogression to a negative fluctuation. During the presence of the light the current remains for half a minute constant; then, upon sudden removal of light, with the same rapidity as at the first oncoming it passes to the zero point and beyond, and finally attains much more

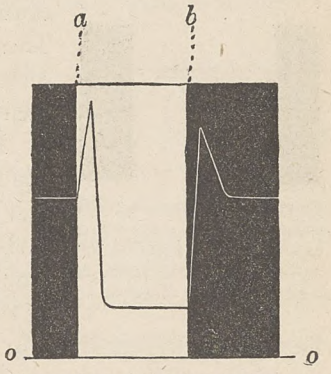
[1] H. U., iii. 3 and 4, S. 327; iv. 1 and 2, S. 1.

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slowly the zero point again. The negative fluctuation may be very great, so that the first positive fluctuation may be considered as only a positive preliminary impulse, and may produce reversal of the current. On the contrary, it may be small, and should then be regarded as the decrement of the first positive fluctuation, this being the case chiefly in very fresh eyes. When the illumination is instantaneous, all three fluctuations are liable to occur. Flickering light tetanizes, as it were, the retina, the phenomenon of superposition being discernible in the first positive fluctuation.

The variation in the direction of the current during absence of light has no influence upon the entrance, course, and magnitude of the photo-electrical fluctuations, except that they all obtain the opposite symbol. This condition is evidently based upon the fact that the anterior and posterior surfaces of the retina, in a condition of excitation, invariably contract to the same differences in tension as had existed before the illumination. The law of the constant alteration of tension suggests that these variations are due to chemical causes.

FIG. 9.



Fluctuations of the electrical current in the isolated retina of a frog when exposed to light.—*a*, oncoming light; *b*, departing light. (Kuehne.)

In order to solve the question how the "visual matters" act towards these fluctuations, investigations have been made on the only verifiable matter, the visual purple, to see how it behaved with and how without the fluctuations. In doing this it was necessary to remember that the unbleached retina is at rest. In order to bring the bleached retina into the same condition, animals must be on ice in the dark, so that regeneration is retarded, —a treatment which is without any influence upon frogs kept in the dark. The magnitude of the fluctuations in unbleached retina was then discovered to be greater for similar irritations than in the bleached, and the irritations in the latter were also altered in quality, being negative to oncoming light, or rarely with the slightest possible positive preliminary impulse.

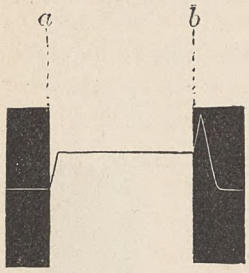
The results obtained by Kuehne and Steiner in isolated retinæ of frogs vary greatly from those which Holmgren, as well as Dewar and McKendrick, had found in the globe. All these observers, however, coincided in the negative fluctuation to oncoming light in rabbits' retinæ. The question then arose, which is the normal condition? It was discovered in the retinæ of rabbits that this simple negative fluctuation probably depended on post-mortem appearances; for, in the first place, the retinæ used had lately rapidly decayed, and in the second place, in the experiments with the frogs' retinæ that had been employed (and which had long remained *in situ*, resulting in alterations which probably depended on suffocation) a stage was discovered in which only a negative fluctuation to oncoming

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light could be discovered. From these results the inference is that it is possible that fresh retinæ from rabbits would act similarly to those of the frog.

As to how the retinal currents act towards bulbar currents, the following conditions were discovered by Kuehne and Steiner. The bulbar current of the frog fluctuates positively to oncoming and to departing light. During the continuance of the light there is no decrement in the first current (which is never seen in the isolated retina) in a course that is for minutes parallel to the abscissa. These results are in opposition to the findings of Dewar and McKendrick, who evidently experimented upon wearied or injured eyes.

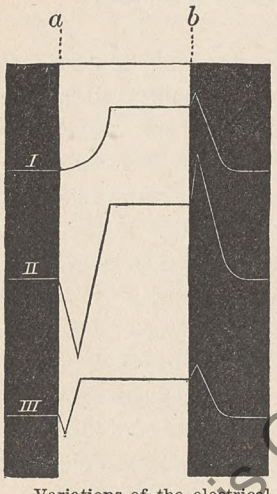
FIG. 10.



Fluctuations of the electrical current in a frog's eye when exposed to the irritation of light.—*a*, oncoming light; *b*, departing light. (Kuehne.)

Here, then, lies a decided difference in comparison with the current of the isolated retina. Kuehne and Steiner found that the anterior segments of the globe could be separated without altering the photo-electrical condition, but if the retina were pulled in the slightest and any vitreous escaped, the same fluctuations appeared as in the isolated retina. The negative fluctuation, therefore, which appears in the latter is a fluctuation of alteration, the cause of which may be sought in an encroachment of the vitreous between the visual cells and the epithelium, which in the globe, perhaps, is not possible to regenerative processes. As shown above, the normal fluctuations of the retinal current in warm-blooded animals may act in the same way as those of the frog. The same may be assumed for bulbar currents, for the results obtained by Dewar and McKendrick on living animals, which do not coincide with this, cannot be employed for comparison, because of the great mutilation of the parts that they permitted in their experiments.

FIG. 11.



Variations of the electrical current in the fresh eyes of fish (*Perca fluviatilis*) when exposed to the irritation of light.—*I*, on the eyeball; *II*, on the hollow shell of the eye; *III*, on the isolated retina; *a*, oncoming light; *b*, departing light. (Kuehne.)

Genuine fluctuations are to be seen in fishes. The induction-current has the same direction as in frogs.

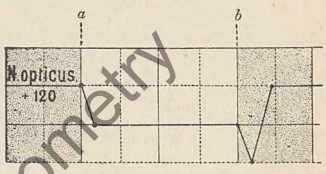
Here the fluctuations to light act as in the hollow shell of the eye, and at first as on the isolated retina. Later many alterations are visible. There is no alteration when the vitreous escapes, because it is more viscid and does not penetrate so easily. The unaltered fluctuations have the following course: with oncoming light they are double: at first they are negative, then positive, in which the later increase surpasses the magnitude of the

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current in darkness whilst the illumination persists. On the departure of the light they are very positive. These fluctuations are evidently the normal ones, for those which differ from them in the entire globe, and which to oncoming light are positive, but increasing very slowly, and persisting during the illumination, and are again positive (though weakly so) on departure, seem to owe these variations to unfavorable conductive conditions, which are easy to understand when the numerous deposits in the backgrounds of fishes' eyes are considered. The first hesitating, positive vibration makes one feel as if all the antagonistic forces which occur in the fluctuation above regarded as normal had simultaneously come to an expression at this point.

As was known to Du Bois-Reymond,[1] the optic nerve of fishes, like all other nerves, gives the legitimate induction-current. Kuehne and Steiner have further found that it gives normal negative fluctuations to electrical irritation. The optic nerve of the frog acts in the same manner. In the frog, however, on account of the minuteness of the nerve, the electrical irritation must be brought close to the peripheral terminal organs in the eye. It is easy, by rapid work during the action of light, to observe on the optic nerve of the frog nothing but a negative fluctuation during oncoming and departing light, as by every other irritation. The optic nerve reacts to continuous light like any other nerve that is exposed to constant irritation. The negative fluctuation is permanent, and the nerve is in a state of phototonus.

FIG. 12.



Variation of the electrical current, under the influence of light, in the optic nerve of the frog.—*a*, oncoming light; *b*, departing light. (Kuehne.)

Some have desired to decide the question whether normal nerves in the eye are free from a current or not. They have attempted this by regarding the visual cells as the natural section of the expansion of the optic nerve. The peculiar photo-electrical vibrations of the rods and cones decidedly refute such a view. Nevertheless, the electrical vibrations are really to be placed in the rods and cones. That they do not lie in the pigment epithelium has been proved by Dewar and McKendrick and by Kuehne and Steiner. Owing to the fact that the opticus must be considered to extend as far as the layer of ganglionic cells, the differences in the photo-electrical processes in the retina and optic nerve compel us to place those processes at least behind the ganglionic cells. Kuehne and Steiner have found that the fluctuations of the optic current in frogs and fishes cease much sooner than those of the retina. From this it might be assumed that the retinal expansion of the optic nerve—*i.e.*, the anterior layers of the retina—no longer reacts to light, and that the still existing fluctuations must be ascribed to the visual cells alone. This conclusion, however, does not hold good in cold-

[1] Untersuch. ü. thier. Elec., ii. S. 256.

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blooded animals, since their optic nerve (and in fishes its expansion into the retina) remains for a long time electrically excitable when the anterior layers of the retina no longer react to light. It thus may happen that the fluctuations to the irritation of light are also situated in the anterior layers of the retina, and, owing to the death of something interpolated between them, can no longer be conducted to the optic nerve. The ganglionic cells of the retina might possibly be regarded as such an interpolation. Kuehne and Steiner, however, have found in pigeons, in whom neither the ganglionic cells nor the nerve-fibres in excised eyes long exist, that they could demonstrate that the retinal fluctuations persist at a time when the above-mentioned connective-tissue elements are dead. This has, moreover, been confirmed by them by special experiments. In such experiments nothing is left as the seat of the vibrations in question but the rods and the cones. In an experiment of Kuehne and Steiner's in which the retina was split into two layers and gently pressed between two silk papers, it was observed that the external members, though fallen into considerable disorder, showed no electrical reaction to the irritation of light, while the other half of the retina still reacted. From this it may be assumed that the photo-electrical processes play their *rôle* chiefly in the interior members of the visual cells.

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